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Gerrit S. Miller Jr.

A

MANUAL OF PALÆONTOLOGY

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A

MANUAL OF PALÆONTOLOGY

FOR THE USE OF STUDENTS

WITH A GENERAL INTRODUCTION ON THE PRINCIPLES OF PALÆONTOLOGY

BY

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AND

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PREFACE.

THERE is, perhaps, no branch of Biology which in recent years has advanced so rapidly, and, on the whole, so surely and in so many directions, as has Palæontology. In the earlier periods of its development, a tendency has, indeed, been sometimes shown by investigators concerned exclusively with existing forms of life to depreciate the position of Palæontology as a Science, and to contest its claims to recognition as a separate department of Zoology and Botany; nor can it be said that this tendency has yet altogether died out. Even now, it is sometimes considered that Palæontology, on the ground of its relation to the chronological history of the earth, should be regarded as a branch of Geology, rather than of Biology; while on the ground of its being necessarily concerned almost wholly with the skeletal structures of animals and plants, its conclusions have been discredited, and the adequacy of its methods of investigation has been questioned.

No one, however, who has made himself thoroughly acquainted with the progress of this branch of investigation during the last decade, can doubt that Palæontology has amply vindicated its claim to be regarded as a special department of Biology, as entirely scientific in its character and methods, and in all respects as worthy of separate and special study as is, for example, the department of Embryology.

So numerous and so extensive have been the advances made by Palæontology of late years, that the Authors have found it necessary not only to largely increase the bulk of the present, as compared with the last, edition of this work; but also to entirely recast and rewrite it, while the illustrations to the text have been nearly

doubled in number. The present edition may therefore be considered as, to all intents and purposes, an entirely new work. The Authors also trust that this edition will be found to have gained much from the fact that the Invertebrates and Vertebrates have been dealt with by different writers.

With regard to the general plan of the work, the Authors need only say that the Invertebrate and Vertebrate animals have been treated of as fully as considerations of space would permit; while the fossil plants have been dealt with in a comparatively summary fashion. This course has been followed primarily on the ground that Palæozoology is of much greater importance to the general student than is Palæobotany; but it has been also dictated by the consideration that the latter subject is one of great complexity, and is at the same time one upon which neither of the Authors has any claim to speak with authority. It did not seem advisable, however, to entirely omit the subject of Palæobotany; and an attempt has accordingly been made to give such a general summary of the present condition of our knowledge of this department as may be found useful to those studying Palæontology as a whole.

In dealing with the vast mass of facts constituting the modern science of Palæontology, much has been, necessarily, omitted; while the Authors can scarcely hope that errors have been altogether avoided. Moreover, in its present condition of rapid growth and development, Palæontology presents many questions—sometimes affecting points of fundamental importance—upon which the opinions of different investigators are widely divergent. It is, therefore, inevitable that there should be many questions dealt with in the present work in regard to which the opinions expressed by the Authors differ from those held by other workers in the same field. The Authors can only hope that on such controverted points they have not expressed themselves too dogmatically; and that, while the limits and scope of the work would not admit of any detailed discussion of divergent views, the existence of such has nevertheless been generally indicated. It may be added that where a definite position has been taken up upon a controverted question, this has been, in general, the result of original investigation on the part of the writer. Theoretical questions, again, have been for the most part avoided, partly because of their unsuitability for discussion in a work intended for students, and partly also from want of

space. Finally, the minute structure of the skeleton in different groups of animals, and particularly in the lower types, has been treated of as fully as the limits of the work have allowed.

Owing to the circumstance that a large portion of the first volume of this work has been in type for a considerable time, the Authors regret that they have not been able to avail themselves fully, or at all, of some recent publications, of both a general and a special nature, such, for example, as Neumayr's 'Die Stämme des Thierreichs,' and the newly published volume of Barrande's monumental work dealing with the Cystideans. In an Appendix to the second volume attention is, however, directed to certain points of importance which have emerged during the passage of this work through the press. Such errors as have been recognised will be found in a list of Corrigenda at the end of the Table of Contents to each volume.

To many of their fellow-workers the Authors have to express their obligation for direct or indirect assistance in their task. To no one is this more largely due than to Professor Karl von Zittel, to whose masterly 'Handbuch der Palæontologie' they have been on many occasions indebted for guidance in questions of doubt or difficulty. The very special gratitude of the Authors is due to Dr P. Herbert Carpenter for the most valuable assistance in the preparation of the chapters dealing with the Echinoderms, as also to Mr A. Smith Woodward and Dr R. H. Traquair for much information concerning fossil Fishes. They have likewise to express their best thanks to Dr George J. Hinde, Dr H. B. Brady, Dr Henry Woodward, Professor T. Rupert Jones, Mr A. H. Foord, Mr John Young, and others of their fellow-workers, from whom they have received much friendly help. Finally, the Authors have to express their gratitude to those who have assisted them by allowing them the use of illustrations. Amongst those to whom thanks are due on this score are M. Louis Dollo, Professors H. F. Osborne and W. B. Scott, Professor A. Gaudry, Professor E. D. Cope, Professor O. C. Marsh, Professor E. Koken, Dr Anton Fritsch, Dr Henry Woodward, the Director of British Museum (Natural History), the present and late Directors of the Geological Survey of India, and the Director of the Geological Survey of Canada.

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CORRIGENDA TO PART II.

Page 397 and page 398, *for* "*Phanerogonia*" and "*Cryptogonia*" *read* "*Phanerozonia*" and "*Cryptozonia.*"

" 451, line 23 from top, *for* "Sporadiporous" *read* "Sporadipodous."

PART I.

GENERAL INTRODUCTION

BY

H. ALLEYNE NICHOLSON

PALÆONTOLOGY.

CHAPTER I.

INTRODUCTION.

Definition of Palæontology.

Palæontology (Gr. *palaios*, ancient; *onta*, beings; *logos*, discourse) is the science which treats of the living beings, whether animal or vegetable, which have inhabited this globe at past periods in its history. It is the ancient life-history of the earth, and if its record could ever be completed, it would furnish us with an account of the structure, habits, and distribution of all the animals and plants which have at any time flourished upon the land-surfaces of the globe or inhabited its waters. From causes, however, which will be subsequently discussed, the palæontological record is most imperfect, and our knowledge is interrupted by gaps which not only bear a large proportion to our solid information, but which in many cases are of such a nature that we can never hope to have them filled up.

As Zoology, then, treats of the animals now inhabiting the earth, and as Botany treats of the now existing plants, Palæontology may be defined as the Zoology and Botany of the past, and may be subdivided into the two subjects of Palæozoology and Palæobotany. The study of fossil animals and plants is, however, based upon the knowledge of living animals and plants, and for this reason Palæozoology and Palæobotany are inseparably connected with Neozoology and Neobotany. The materials, again, which fall to be studied by the palæontologist, are drawn entirely from the proper province of the geologist. *Fossils* are derived from *rocks*. It will therefore be necessary to trespass to some extent upon the peculiar domain of the geologist, and to obtain some knowledge of the origin, com-

position, and mode of occurrence of the rocks from which Palæontology obtains its materials. Lastly, Palæontology, apart from its own importance as an independent branch of Zoology, is employed by the geologist to assist him in his determination of the chronological succession of the materials which compose the crust of the earth. Palæontology, therefore, in one of its aspects, is a branch of geological science, and requires separate study in its relation to historical Geology.

Definition of Fossils.

All the natural objects which come to be studied by the palæontologist are termed "fossils" (Lat. *fossus*, dug up). In most cases, fossils, or, as they are often termed, "petrifactions," are actual portions of animal or vegetable organisms, such as the shells of Molluscs, the skeletons of Corals, the bones of Vertebrate animals, the wood, bark, or leaves of plants, &c.; and these may be preserved very much in their original condition, or may have been very much altered by changes subsequent to their burial. Strictly speaking, however, by the term "fossil" is understood "any body, *or the traces of the existence of any body*, whether animal or vegetable, which has been buried in the earth by natural causes" (Lyell). We shall find, therefore, that we must include under the head of fossils objects which at no time themselves formed parts of any animal or vegetable, but which, nevertheless, point to the former existence of such organisms, and enable us to reason as to their nature. Under this head come such fossils as the moulds or "casts" of shells and the footprints or markings left by various animals upon sand or mud.

In the great majority of cases fossils are the remains of animals or plants which are now *extinct*—that is to say, which no longer are in existence, but have entirely disappeared from the earth's surface. In some cases, however, fossils are the remains of *recent* animals—that is, of animals which are still found in a living condition upon the globe. The term "sub-fossil," sometimes applied to these, has been more appropriately applied in another sense, and is best discarded in this connection. In any case, the fact that a given specimen belongs to an extinct species of animal or plant, or that it is referable to some existing form, does not enter in any way whatever into the determination of the question as to whether or not it is truly a *fossil*. If such a specimen is found in those portions of the earth's crust which we can show by other evidence to have been formed prior to the establishment of the existing terrestrial order, then it is a fossil; while any remains, even though belonging to the same animal, which are found in deposits which have been formed during the historical period, would be, strictly speaking, referred to

the domain of the neozoologist or the neobotanist, and would not rightly be termed "fossils." It must be admitted, however, that in approaching the "Recent" period of the earth's history, it becomes a matter of difficulty—in some cases an impossibility—to draw any precise line between fossil and recent specimens.

The terms "fauna" and "flora" are employed in Palæontology much as they are by the student of recent forms, to mean the entire assemblage of the animals or of the plants respectively belonging to a particular region or a particular time. Thus we may speak of the "fauna" of the Carboniferous Period, or the "flora" of the Tertiary Epoch, or the fauna of the Chalk, or of any other set of beds.

Fossilisation.

The term "fossilisation" may be applied in a general sense to all the processes through which an organic body passes in order to become a fossil. Here we need only consider the three leading forms in which fossils present themselves. In the first instance, the fossil is to all intents and purposes an actual organic remain, being itself a fragment of an animal or plant. Thus we may meet with fossil bones, shells, or wood, which may have undergone certain changes, such as would be produced by pressure, by the deprivation of organic matter originally present, or by more or less complete infiltration with mineral matter, but which, nevertheless, are practically the real bodies they represent. As a matter of course, it is in the more modern formations that we find fossils least changed from their primitive condition, but almost all formations contain some fossils in which the original structure is more or less completely retained.

In the second place, we very frequently meet with fossils in the state of "casts" or moulds of the original organic body. What occurs in this case will be readily understood, if we imagine any common bivalve shell, as an Oyster, or Mussel, or Cockle, embedded in clay or mud. If the clay were sufficiently soft and fluid, the first thing would be that it would gain access to the interior of the shell and would completely fill up the space between the valves. The pressure, also, of the surrounding matter would ensure that the clay would everywhere adhere closely to the exterior of the shell. If now we suppose the clay to be in any way hardened so as to be converted into stone, and if we were to break up the stone, we should obviously have the following state of parts. The clay which filled the shell would form an accurate cast or mould of the *interior* of the shell, and the clay outside would give us an exact impression or cast of the *exterior* of the shell (fig. 1). We should have, then, two casts, an interior and an exterior, and the two would be very different from one another, since the inside of a shell is very unlike the

outside. In the case, in fact, of many Molluscan shells, the interior cast is so unlike the exterior or unlike the shell itself, that it may be difficult to determine the true origin of the former.

It only remains to add that there is sometimes a further complication. If the rock be very porous and permeable by water, it may happen that the original shell is entirely dissolved away, leaving the interior cast or "mould" loose, like the kernel of a nut, within the case formed by the exterior cast. Or it may happen that subsequent to the attainment of this state of things, the space thus left vacant between the interior and exterior cast—the space, that is, formerly occupied by the shell itself — may be filled up by some foreign mineral deposited there by the infiltration of water. In this last case the splitting open of the rock would reveal an interior cast, an exterior cast, and finally a body which would have the exact form of the original shell, but which would really be of much later origin and would not exhibit under the microscope the minute structure of shell.

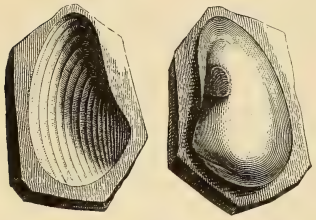


Fig. 1.—*Trigonia longa*, showing casts of the exterior and interior of the shell. Neocomian.

In the third class of cases we have fossils which present with the greatest accuracy the external form, and sometimes even the internal minute structure, of the original organic body, but which, nevertheless, are not themselves truly organic, but have been formed by a "replacement" of the particles of the primitive organism by some mineral substance. The most beautiful example of this is afforded by fossil wood which has been "silicified" or converted into flint. In this case we have a piece of fossil wood, which presents the rings of growth and fibrous structure of wood, and under the microscope exhibits even the minutest vessels which characterise ligneous tissue. The whole, however, instead of being composed of the original carbonaceous matter of the wood, is now converted into pure flint. The only explanation which can be given of this by no means very rare phenomenon, is that the wood must have undergone a slow process of decay in water holding silica or flint in solution. As each particle of the wood was removed by decay, its place was taken by a particle of flint deposited from the surrounding water, till ultimately the entire wood was silicified. The replacing substance is by no means necessarily flint, but may be iron-pyrites, oxide of iron, sulphur, malachite, magnesite, talc, &c.; and it is not uncommon to find many other fossils besides wood preserved in this way, such as shells, corals, or sponges.

The *replacement* of the original substance of a fossil by some

foreign body is thus a matter of common occurrence, but it is by no means always easy to determine whether or not such replacement has taken place. By far the commonest mode of replacement is that whereby an originally calcareous skeleton is replaced by silica. This process of "silicification"—of the replacement of *lime* by *silica*—is not only an extremely common one, but it is also a readily intelligible one; since carbonate of lime is an easily and flint a hardly soluble substance. It is thus easy to understand that originally calcareous fossils, such as the shells of Mollusca, or the skeletons of Corals, should have in many cases suffered this change, long after their burial in the rock, their carbonate of lime being dissolved away, particle by particle, and replaced by precipitated silica, as they were subjected to percolation by heated or alkaline waters holding silica in solution.

In a large number of cases of silicification, the minute *structure* of the fossil which has been subjected to this change is found to have been more or less injuriously affected, and may be altogether destroyed, even though the *form* of the fossil be perfectly preserved. This is the rule where the silicification has been secondary, and has taken place at some period long posterior to the original entombment of the fossil in the enveloping rock; whereas if the original fossilisation has been effected by infiltration with silica in the first instance, then the minute structure is usually perfectly preserved. In secondary silicification, as seen in corals and shells, the carbonate of lime of the original fossil is gradually more or less completely replaced by silica, the process beginning on the exterior and gradually extending inwards. In the first stage of the process, the outer layer of the fossil very commonly becomes more or less largely converted into, or covered by, small circular deposits of silica, having the form of a central boss surrounded by one or more concentric rings ("orbicular silica" or "Beekite markings"). If the process goes on, the whole of the fossil may ultimately become converted into flint. Secondarily silicified fossils, though ill adapted for microscopic examination, are often of great beauty, as they commonly "weather out" from the more readily soluble limestone in which they are embedded, and can thus be obtained in absolute entirety.

When we meet with fossils, such as those alluded to above, which we *know* to have been originally calcareous, but which we now find, unchanged in form, although converted into flint, then we cannot doubt that we have to deal with cases of "silicification," and that the primitive skeleton of lime has in these cases been slowly, and more or less perfectly, replaced by silica. We cannot, however, speak in such a positive manner as to fossils which we now find to be composed of flint, but as to the original constitution of which we cannot be certain. We find, namely, some fossils which are of uncertain affinities, and which sometimes occur in a siliceous and sometimes in a calcareous state. If we are not positive as to the zoological position of these fossils, or if they belong to a group of animals in

which we find the living forms to possess sometimes a calcareous and at others a siliceous skeleton, then it is obviously a matter of extreme difficulty to determine whether the extinct forms were really composed of lime or of flint. In such cases, we must be guided principally by the condition of preservation of the fossils which occur associated with such obscure forms in the same beds; the fact that the associated remains are converted into flint pointing to the probability that the problematical forms were originally calcareous, and *vice versâ*. In the case, also, of all fossils which present themselves sometimes in a siliceous and sometimes in a calcareous form, there is always the *presumption* that the skeleton was originally composed of *lime*, this presumption being based upon the fact that the conversion of the calcareous skeletons of animals into silica by a process of replacement is an unquestionable, an extremely common, and a readily intelligible occurrence.

Until recently, indeed, naturalists never allowed themselves to contemplate the alternative possibility of an originally *siliceous* skeleton being replaced by *lime;* but we have now unequivocal evidence that this anomalous mode of replacement is of not very uncommon occurrence. The researches of Zittel, Hinde, and Sollas have, in fact, proved that the colloid silica of the siliceous skeletons of the Flinty Sponges is comparatively unstable, and that under certain circumstances it can be readily dissolved in water. Hence these Sponges are commonly found in the fossil condition with the silica of the original skeleton more or less extensively replaced by carbonate of lime, or by oxide or sulphide of iron. When the replacing agent is lime, it is found not only that the microscopic structure of the original skeleton has been completely lost; but that the lime is always in the *crystalline* condition, consisting of unoriented crystals of calcite. This latter fact affords conclusive proof that the skeleton was not primitively calcareous, but that the lime is of secondary origin and has replaced some other material

In any case we must carefully distinguish between *replacement*, whether by flint or any other mineral, and *infiltration*, the latter being merely the process whereby the cavities and natural vacuities of a fossil are liable to become filled by some mineral substance, subsequent to its entombment in sediment. When such a fossil as a shell or a coral, for example, becomes buried in the sandy, calcareous, or argillaceous mud at the bottom of the sea, the surrounding sediment often does not penetrate into the deeper parts of the fossil, and there are thus left in its interior certain empty spaces, into which the surrounding water makes its way by percolation. Any mineral substances, such as carbonate of lime or silica, which may be contained in solution in the water, are then liable to undergo precipitation, and to be deposited in a solid form within the fossil.

All the natural cavities of a fossil, even down to the minutest microscopic pores or tubes, may in this way become filled with some such infiltrated material, the two commonest agents in this process being lime and flint. If the skeleton of the fossil be a calcareous one, while the infiltrating material has been some less soluble substance, such as silica or some silicate, then the skeleton may be artificially or naturally dissolved away, leaving a *cast* of the internal cavities of the fossil formed of the infiltrated matter. Thus the minute shells of *Foraminifera* are often infiltrated with the silicate glauconite, and exquisitely perfect casts of their interior cavities are subsequently formed by dissolution of the shell itself. In this way, as we shall see hereafter, deposits of greensand have been sometimes produced.

Definition of Rock.

The crust of the earth consists of various different materials, produced at different successive periods, occupying certain definite spaces, and not confusedly mixed together, but, on the contrary, exhibiting a definite and discoverable order of arrangement. All these materials, however different in appearance, texture, or mineral composition, are called "rocks" by the geologist. The term "rock," then, is to be understood as applying to *all* the materials which compose the crust of the earth. In the language of geology, the finest mud, the loosest sand, and the most incoherent gravel, are just as much *rocks* as are the hardest and most compact granites or limestones.

Classification of Rocks.

For the purposes of the palæontologist all the rocks which enter into the composition of the solid exterior of the earth may be divided into two great classes: 1. The Igneous Rocks, which are formed within the body of the earth itself, and owe their structure and origin to the action of heat; and 2. the Aqueous or Sedimentary Rocks, which are formed at the surface of the earth, and owe their structure, at any rate in part, to the mechanical action of water. The Igneous Rocks are principally formed below the surface of the earth, are as a general rule destitute of organic remains or fossils, and are mostly in the form of *unstratified* masses. The Aqueous and Sedimentary Rocks are formed at the surface by the disintegration and reconstruction of previously existing rocks, or by the vital chemistry of animals or plants, are mostly fossiliferous, and are *stratified*—*i.e.*, are arranged in distinct layers or "strata." The Aqueous Rocks, as containing fossils, are the only rocks with which it is essential for the palæontologist to be acquainted, and we shall very briefly consider their leading physical characters, their

chief varieties, their mode of origin, and their historical succession. It should be borne in mind, however, that there are cases in which strictly volcanic deposits may come to contain the remains of animals and plants. Thus, animals and plants may be enveloped and entombed in showers of volcanic ashes falling upon land, and deposits of subaerial volcanic ash may thus become fossiliferous. Moreover, it is very common for volcanic ashes to fall in vast quantities into the sea or into a lake, when they become subjected to the action of water, and may envelop the animals living at the bottom. Hence it is by no means unusual to meet in the crust of the earth with more or less extensive deposits of volcanic ashes, which though igneous in origin are secondarily aqueous, being not only stratified but also containing the remains of aquatic animals.

CHAPTER II.

THE FOSSILIFEROUS ROCKS.

The Sedimentary or Fossiliferous Rocks form the greater portion of that part of the earth's crust which is open to our examination, and are distinguished by the fact that they are regularly "stratified," or arranged in distinct and definite layers or "strata." These layers may consist of a single material, as in a block of sandstone, or they may consist of different materials. When examined on a large scale, they are always found to consist of alternations of layers of different mineral composition. We may examine any given area, and find in it nothing but one kind of rock—sandstone, perhaps, or limestone. In all cases, however, if we extend our examination sufficiently far, we shall ultimately come upon different rocks; and, as a general rule, the thickness of any particular set of beds is comparatively small, so that different kinds of rock alternate with one another in comparatively small spaces.

As regards the origin of the Sedimentary Rocks, they are for the most part "derivative," being derived from the wear and tear of pre-existent rock. Sometimes, however, they owe their origin to chemical or vital action, when they would more properly be spoken of simply as Aqueous Rocks. As to their mode of deposition, we are enabled to infer that the materials which compose them have formerly been spread out by the action of water, from what we see going on every day at the mouths of our great rivers, and on a smaller scale wherever there is running water. Every stream, where it runs into a lake or into the sea, carries with it a burden of mud, sand, and rounded pebbles, derived from the waste of the rocks which form its bed and banks. When these materials cease to be impelled by the force of the moving water they sink to the bottom, the heaviest pebbles, of course, sinking first, the smaller pebbles and sand next, and the finest mud last. Ultimately, therefore, as might have been inferred upon theoretical grounds, and as is proved by practical experience, every lake becomes a receptacle for a series

of stratified rocks produced by the streams flowing into it. These deposits may vary in different parts of the lake, according as one stream brought down one kind of material and another stream contributed another material; but in all cases the materials will bear ample evidence that they were produced, sorted, and deposited by running water. The finer beds of clay or sand will all be arranged in thicker or thinner layers or laminæ; and if there are any beds of pebbles these will all be rounded or smooth, just like the water-worn pebbles of any brook-course. In all probability, also, we should find in some of the beds the remains of fresh-water shells, plants, or other organisms which inhabited the lake at the time these beds were being deposited.

In the same way large rivers—such as the Ganges or Mississippi—deposit at their mouths much of the material which they bring down, forming in this way their "deltas." Whenever such a delta is cut through, either by man or by some channel of the river altering its course, we find that it is composed of a succession of horizontal layers or strata of sand or mud, varying in mineral composition, in structure, or in grain, according to the nature of the materials brought down by the river at different periods. Such deltas, also, will contain the remains of animals which inhabit the river, with fragments of the plants which grew on its banks, or bones of the animals which lived in its basin.

Lastly, the sea itself—irrespective of the materials delivered into it by rivers—is constantly preparing fresh stratified deposits by its own action. Upon every coast-line the sea is constantly eating back into the land and reducing its component rocks to form the shingle and sand which we see upon every shore. The materials thus produced are not, however, lost, but are ultimately deposited elsewhere in the form of new stratified accumulations, in which are buried the remains of animals inhabiting the sea at the time.

Whenever, then, we find anywhere in the interior of the land any series of beds having these characters—composed, that is, of distinct layers, the particles of which, both large and small, show distinct traces of the wearing action of water—whenever and wherever we find such rocks, we are justified in assuming that they have been deposited by water in the manner above mentioned. Either they were laid down in some former lake by the combined action of the streams which flowed into it; or they were deposited in some portion of the course of an ancient river; or they were laid down at the bottom of the ocean. In the first two cases, any fossils which the beds might contain would be the remains of fresh-water or terrestrial organisms. In the last case, the majority, at any rate, of the fossils would be the remains of marine animals.

The term "formation" is often employed by geologists in a loose

general sense to signify "any group of rocks which have some character in common, whether of origin, age, or composition" (Lyell); so that we may speak of stratified and unstratified formations, aqueous or igneous formations, fresh-water or marine formations, and so on.

Chief Divisions of the Aqueous Rocks.

The Aqueous Rocks may be divided into two great sections, the Mechanically-formed and the Chemically-formed, including under the last head all rocks which owe their origin to vital action, as well as those produced by ordinary chemical agencies. It must not be forgotten, however, that such a division, though convenient in practice, is largely artificial. Thus many organically-formed rocks are to a large extent the product of mechanical action, since, though consisting of the skeletons of organisms, their component materials have been mechanically broken down and transported by water. Moreover, no sharp line of demarcation can be drawn between the above two groups of rocks, innumerable transitions existing between rocks which are purely mechanical in origin and those which are the direct result of vital action.

A. Mechanically-formed Rocks.—These are all those Aqueous Rocks of which we can obtain proofs that their particles have been mechanically transported to their present site. Thus, if we examine a piece of conglomerate or pudding-stone, we find it to be composed of a number of rounded pebbles embedded in an enveloping paste or matrix. The pebbles are worn and rounded, and thus show that they have been subjected to much mechanical attrition, whilst they have been mechanically transported for a greater or less distance from the rock of which they originally formed part. In the case of an ordinary sandstone, the component grains of sand are equally the result of mechanical attrition, and have been equally transported from a distance. In the case of still finer rocks, such as shale, the particles have been so much water-worn that their source cannot be recognised, though a microscopical examination would reveal that their edges were all worn and rounded. It follows from this that the mechanically-formed Aqueous Rocks are such as can be proved to have been *derived* from the abrasion of other pre-existent rock: hence they are often spoken of as "Derivative Rocks." Every bed, therefore, of any mechanically-formed rock, is the equivalent of a corresponding amount of destruction of some older rock.

The mechanically-formed Rocks may be divided into the two groups of the Arenaceous or Siliceous Rocks, and the Argillaceous or Aluminous Rocks. In the Arenaceous group are those Aqueous Rocks which are mainly composed of smaller or larger grains of flint or silica. The chief varieties are the various kinds of sand and

sandstone, grits, and most conglomerates and breccias. In the Argillaceous group are those Aqueous Rocks which contain a certain amount of clay or hydrated silicate of alumina. Under this head come clays, shales, marls, clay-slate, and most flags or flagstones. In nature there exists, it need hardly be said, no rigid line which separates the Arenaceous from the Argillaceous rocks. The two groups are connected together by endless transitional forms, and we must regard all the mechanically-formed rocks as variable mixtures of different ingredients, their precise character depending on the predominance of some one constituent.

B. Chemically-formed Rocks.—In this section are comprised all those Aqueous Rocks which have been formed by chemical agencies. Since, however, many of these chemical agencies are exerted through the medium of living beings, whether animals or plants, we get into this section a number of what may be called "organically-formed" rocks. The most important of the Chemically-formed Rocks are the so-called Calcareous Rocks, comprising all those which contain a large proportion of carbonate of lime, or are wholly made up of this substance; but there are other rocks, of different composition, formed by chemical or organic agency, which may be briefly noticed.

As an example of a rock the origin of which is purely chemical, we may take *rock-salt* or *sodium chloride*, extensive deposits of which occur in formations of all ages, from the Silurian upwards. Whatever may have been the precise mode in which these deposits were formed, it is quite certain that the salt existed, to begin with, in solution in water, and that its assumption of the solid form was the result simply of precipitation. Hence, rock-salt is invariably composed of larger or smaller crystals of sodium chloride, though not uncommonly rendered impure by intermixture with sand or clay.

Another rock which may be regarded as a direct product of chemical action, apart from the operation of living beings, is *gypsum* or *calcium sulphate*. This substance, apart from other modes of occurrence, is not uncommonly found interstratified with the ordinary sedimentary rocks, in the form of more or less irregular beds; and in these cases it has a certain palæontological importance, as occasionally yielding well-preserved fossils. In general appearance, gypsum, when occurring in mass, is usually a whitish, yellowish, or reddish granular rock, which can be easily shown by the microscope to be composed of crystals of calcium sulphate. Very commonly, indeed, the rock is as coarsely crystallised as loaf-sugar, or more so, and the microscope is not needed for the recognition of its true structure. With regard to its mode of origin, there is no reason to doubt that deposits of gypsum are formed by the direct precipitation of calcium sulphate from solution in water, without the inter-

vention of living beings; though it is possible that in some cases the chemical changes which have resulted in the production of masses of gypsum may have been secondary, and may have acted at some period posterior to the original deposition of the rocks associated with these.

Another lime-salt which owes to chemical action its present form, and its present relations to the rocks with which it is associated, is *phosphate of lime*. Calcium phosphate occurs in the form of larger or smaller crystals (apatite) in many crystalline rocks, whether these be metamorphic or igneous in origin. It also sometimes occurs in considerable beds (phosphorite) in formations of various ages; and it occurs abundantly in the form of nodules in some parts of the Secondary and Tertiary deposits. It likewise may occur disseminated through the ordinary stratified rocks in such a condition as not to be capable of detection save by chemical analysis, as has been shown by Dr Hicks in the case of the Cambrian rocks of Wales. When it is found in the crystalline or in the massive condition, there is no reason to doubt that calcium phosphate is the product of direct chemical action. Even in these cases, however, it is quite possible that it may have been sometimes derived in the first place from the skeletons or excrements of animals. Phosphate of lime forms the larger proportion of the earthy matter of the bones in Vertebrate animals, and also occurs in less amount in the skeletons of certain of the Invertebrates (*e.g.*, *Lingula* and *Discina*, among the Brachiopods; *Conularia* and *Hyolithes*, among the Pteropods; and the *Crustacea* in general). Phosphate of lime is thus, perhaps even more distinctively than carbonate of lime, an organic compound. When calcium phosphate occurs minutely disseminated through a rock, it is tolerably certain that it has been derived from animals and plants. It is also almost certain that the phosphate of lime in the so-called "coprolites" of the Cambridge Greensand, as in other similar phosphatic nodules, is organic in origin. Some of these nodules consist of organisms, such as Sponges, infiltrated with phosphate of lime, but most of them would seem to have been formed by a process of segregation similar to that which has given rise to nodules of clay-ironstone or of carbonate of lime in beds of shale. The name of "coprolites" given to these phosphatic nodules is founded upon a misconception, as they are not actually the fossilised excrements of animals. In various formations, however, there are found genuine "coprolites"—*i.e.*, the petrified excreta of Fishes, Reptiles, or Mammals,—and these are largely composed of phosphate of lime.

By far the largest and most important group of the chemically-formed rocks is that of the *Calcareous Rocks*, comprising all those rocks in which carbonate of lime is the predominating ingredient, and which are therefore spoken of by the general name of *limestones*.

In all cases, the carbonate of lime which exists in a limestone has previously existed in solution in water, either in the water of a spring, river, or lake, or in that of the ocean itself. Owing, in fact, to the ready solubility of calcium carbonate in water holding in solution a certain proportion of carbon dioxide, a larger or smaller quantity of this mineral is invariably found dissolved in all natural waters, whether fresh or salt, since these waters are always to some extent charged with this solvent gas. There are two principal methods by which the carbonate of lime held in solution in water may again assume the solid form. One of these methods consists in the chemical precipitation of the carbonate of lime from the water. This takes place whenever the carbonic acid in the water becomes so far reduced in quantity that it is no longer able to retain in solution all the lime that had been previously dissolved; or whenever the water undergoes partial or complete evaporation; or, again, when water which had been enabled by a high temperature to take up an excess of lime, is subjected to cooling. Various well-known calcareous deposits, such as the "stalactites" and "stalagmites" of limestone caves, and the "calcareous tufa" and "travertine" of springs, are produced in this way by the direct precipitation of carbonate of lime from solution. All limestones deposited in this chemical way directly from saturated solutions are necessarily composed of larger or smaller crystals of carbonate of lime, and the microscope will show that their structure is more or less clearly *crystalline*. They may contain the remains of animals or plants, as is not uncommon in the spongy calcareous tufa deposited by "petrifying springs"; but as such remains are usually only *encrusted* by the precipitated lime, and are not infiltrated, they generally become dissolved out in the course of time, leaving cavities which mark their former presence. Calcareous deposits formed by direct precipitation occasionally occur on a large scale, and thus become geologically important, but the ordinary limestones are formed in a different way, and are of much greater palæontological interest.

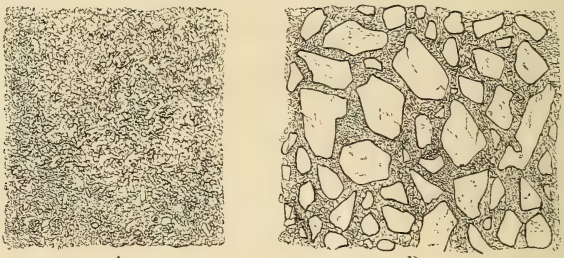
By far the most general method in which the dissolved carbonate of lime in water may be converted into the solid form is by the vital chemistry of animals and plants. Very many animals, and a considerable number of plants, have the power of abstracting from the water the carbonate of lime which it holds in solution, and of building up in this way a calcareous skeleton. Hence, while the waters which percolate through the earth's crust are constantly taking up fresh carbonate of lime, this is being as constantly removed from the waters of rivers, lakes, and the sea, and again converted into the solid form, by the agency of living beings. It is owing to the fact that animal life is much more abundant in the sea than in rivers and lakes, that sea-water contains a proportionately smaller proportion of

dissolved lime than fresh waters, in spite of the circumstance that rivers are constantly pouring into the sea vast quantities of this substance.

Considering the constant production of carbonate of lime by various animals and plants, it is not surprising to find on investigation that many limestones are more or less extensively composed of the skeletons of living beings. Most limestones are therefore, more or less clearly, *organic* rocks. There are, however, two methods—not always very clearly separated from one another—in which an organic limestone may be formed. In one set of cases, the limestone is the result of the accumulation of the calcareous skeletons of animals in the place where these organisms actually lived and grew. This is seen occasionally where a limestone has been formed by the growth of innumerable generations of sedentary Molluscs, such, for example, as Oysters. Some Crinoidal limestones have also been formed by the accumulation of Crinoids in place; and many of the more modern coral-limestones are similarly the result of the growth of the lime-producing polypes in the locality where we now find the rock. In another and more extensive set of cases, the limestone has been formed by the gradual accumulation of the skeletons of animals or plants which lived in some place more or less widely removed from that occupied by the limestone itself. Thus, extensive calcareous deposits may be formed at the bottom of the deep sea by the slow accumulation of the calcareous skeletons of animals which live at the surface of the ocean, and the shells of which fall to the bottom on the death of the animal which produced them. This is seen in certain Foraminiferal limestones and in Pteropodal limestones, though in all such cases the rock is in part made up of the skeletons of animals which actually lived at the bottom of the sea. In other cases, the calcareous skeletons of animals are thrown up in great banks by the action of the sea in the neighbourhood of land. This is the case, for example, with the great accumulations of shell-sand on many parts of our shores, or with the still more extensive deposits of coral-sand in warm seas. In such cases, the limestone is so far *organic* that it is formed mainly out of the skeletons of lime-secreting animals or plants, but it is also so far *mechanical* that the actual formation of the limestone has been due to the breaking up and wearing down of these skeletons by the movements of the waves of the sea.

If this wearing-down action has been sufficiently long-continued and sufficiently complete, we may not be able to recognise in the limestone many, or indeed any, actual fragments of shells or other animal structures; but the rock may appear under the microscope as a fine-grained calcareous mud, made up of minute, mostly non-crystalline granules of carbonate of lime (fig. 2, A). This is the case, for

example, with some limestones of quite recent date, and with the so-called "lithographic" limestones of various geological periods from the Ordovician onwards. Similar fine-grained calcareous muds may likewise be formed by the slow digestion and consequent disintegration of the calcareous skeletons of animals and plants, which takes place when such skeletons are long exposed to the action of sea-water. In other cases, again, a calcareous mud of the kind here spoken of may be produced by the wearing down of previously exist-



A B

Fig. 2.—A, Thin section of lithographic limestone, Jurassic, Solenhofen, greatly magnified. The rock is a fine-grained calcareous mud, for the most part non-crystalline. B, Thin section of an arenaceous limestone from the Middle Permian of Westmorland. The rock is largely mechanical in origin, angular fragments of quartz being cemented together by a crystalline dolomitic matrix. (Original.)

ing limestones. More commonly the abrasive action of the sea has not been sufficiently prolonged or severe to reduce the calcareous fragments to the form of mere calcareous grains, in which the organic structure is no longer perceptible. Hence the great majority of limestones, when examined microscopically, are found to consist of more or less complete skeletons, or portions of the skeletons, of different kinds of lime-producing animals or plants, cemented together by a general crystalline or granular matrix. The general mode of origin of such limestones is rendered sufficiently clear by an investigation of calcareous deposits now in process of formation. Such a limestone to begin with exists in the form of an accumulation of entire or fragmentary calcareous skeletons, of all shapes and sizes, loosely heaped together, and more or less extensively separated by vacant spaces. In the process of consolidation, the irregular lacunæ between the component fragments of the mass may become infiltrated with fine calcareous mud, produced by the disintegration and wearing down of the superficial portions of the mass; and the resulting rock will then have the structure of a granular matrix enclosing innumerable entire or fragmentary organisms. An excellent example of such a rock is to be obtained in the White Chalk (fig. 3), which consists of innumerable organic fragments, mostly referable to the

Foraminifera, cemented together by a fine calcareous mud, and which was probably formed in water of considerable depth. In the more ordinary limestones—most of which have been formed close to a shore-line—the original accumulation of partially broken-up calcareous skeletons is subjected to the percolation through its mass of water holding carbonic acid in solution. As the result of this, partial solution of the mass takes place, and the dissolved carbonate of lime is ultimately deposited in the form of calcite, the rock thus

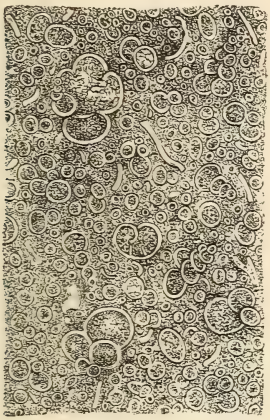


Fig. 3.—Thin section of White Chalk, from Sussex, enlarged about fifty times. The matrix is a calcareous mud, and the contained organisms are mostly entire or broken Foraminifera. (Original.)

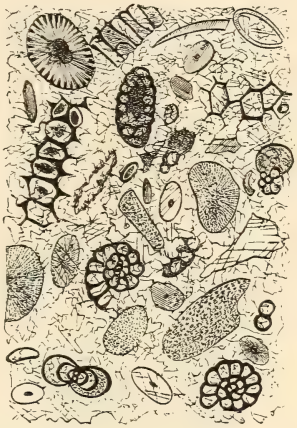


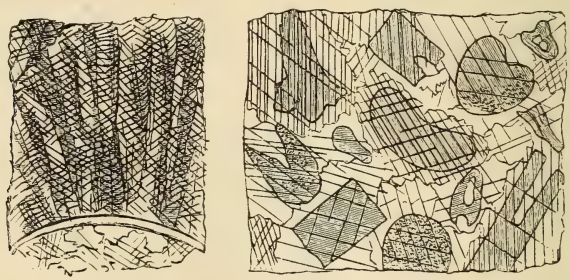
Fig. 4.—Thin section of Carboniferous limestone, from Shap, enlarged about fifteen times. The matrix is crystalline, and the included organisms are Foraminifera, calcareous Algæ, joints of Crinoids, &c. (Original.)

assuming the character of a congeries of organic fragments bound together by a general matrix of crystalline carbonate of lime (fig. 4). Even accumulations of sand may be in this way subjected to the percolation of acidulated water holding lime in solution, and may thus be converted into arenaceous limestones, in which angular quartz-grains are united by a matrix of crystalline carbonate of lime (fig. 2, B). The microscope shows us that very many of the limestones composing the crust of the earth, of all geological ages except the most ancient, have been formed in the general method above described. Limestones of essentially similar structure are also now in process of formation on a large scale. This is specially seen in the warm seas of the coral-region, where the broken down coral-sand commonly becomes converted in time into a hard, crystalline or semi-crystalline limestone; and we may occasionally see the same process at work, on a smaller scale, in the shell-sand of our own shores.

It follows from the above, that the formation of the crystalline matrix of an ordinary limestone is always secondary to the accumulation of the

organic fragments which compose the mass of the rock. In some cases the matrix has been deposited in the first instance in a crystalline form, and is the result of the percolation through the mass of water charged with carbonate of lime in solution. In other instances, the matrix has, to begin with, been composed of a fine calcareous mud, which has later undergone crystallisation, as the result of secondary chemical and mechanical changes. Sometimes this superinduced crystallisation may be the result of pressure; in other cases it may be caused by the percolation through the rock of heated or carbonated water; while in many instances it is connected with the process of dolomitisation.

In this process of superinduced crystallisation, the organic fragments contained in the rock usually show themselves more stable than does the matrix. Hence the matrix may become more or less highly crystalline, while the included organic fragments remain more or less distinct and unaffected. It often happens, however, as specially insisted upon by Dr Sorby, that the fragments of calcareous organisms have crystallised along with the surrounding matrix, in such a manner as to have more or less extensively lost not only their organic structure but also their external outline. There are various degrees in which this superinduced crystallisation, and consequent obliteration, of the included organic fragments in a limestone takes place. It is noticeable, however, that the agencies which give rise to this condition are not necessarily of any great intensity, since complete crystallisation and obliteration of the included organic remains may occur in modern calcareous deposits (*e.g.*, some coral-lime-



B A

Fig. 5.—A, Section of Ordovician limestone, from Keisley, Westmorland, in which the crystallisation of the matrix has extended to the included fragments of Crinoids, as shown by the continuation of the cleavage-planes from one to the other. Enlarged about five times. B, Fibro-crystalline structure developed in the same limestone, considerably enlarged. (Original.)

stones). An interesting example of this phenomenon is commonly seen in Crinoidal limestones, in which the entire rock may be so crystallised that the cleavage-planes of the calcite run continuously through both the matrix and the included fragments of Crinoids, the latter nevertheless preserving their outlines (Fig. 5, A.)

In many of the older limestones, portions of the rock often exhibit a peculiar fibro-crystalline structure, being composed of feather-like columns of crystalline carbonate of lime, placed side by side and intersected by a double cleavage. Sections of such fibro-crystalline masses (Fig. 5, B), examined microscopically, commonly show, therefore, a characteristic pinnate or "herring-bone" structure, due to the crossing of the two sets of cleavage-planes. This remarkable structure is obviously the

result of secondary changes affecting the limestone. It is of frequent occurrence in the calcareous material which occupies the interior of fossils, such as the shells of Mollusca or the crusts of Trilobites, in which case the columns radiate from the surface of attachment. In other cases, it occupies irregular winding spaces in the rock, when it exhibits a concentrically banded structure, indicating its formation in successive layers, while the constituent fibres radiate inwards in all directions from the bounding surfaces of the mass. Under ordinary conditions, this peculiar fibro-crystalline structure can only be regarded as purely inorganic. In some instances, however, an apparently identical structure is produced by the partial crystallisation of organic remains, such as the calcareous skeletons of Stromatoporoids or Corals. It would appear that the so-called *Stromatactis* of Monsieur E. Dupont, which plays a very important part in the formation of some of the Devonian limestones of Belgium, is really of the nature of the above-mentioned fibro-crystalline masses, being partly of inorganic origin, and probably in part the result of secondary change in suitable fossils, such as Stromatoporoids.

Any of the great groups of Invertebrates in which a calcareous skeleton is produced may take a more or less prominent part in the formation of a limestone; and the principal facts connected with this subject will be dealt with in greater detail in treating of each group of animals separately. It may be well, however, to indicate here, in the briefest manner, the chief groups of organisms, whether animal or vegetable, which may be considered as pre-eminently makers of limestones. As regards animals, a very important place must be assigned to the *Foraminifera*, a group of the *Protozoa* in which a calcareous shell is commonly developed. So far as the older Palæozoic limestones (Ordovician, Silurian, and Devonian) are concerned, it is noteworthy that in very few instances, so far as yet known, do the tests of *Foraminifera* constitute a prominent constituent of the rock. In all the later formations, however, beginning with the Carboniferous, we meet with limestones which are more or less highly charged with the calcareous tests of these minute organisms, sometimes in such numbers that the rock becomes what may be properly called a "Foraminiferal limestone" (fig. 6). Of this nature are the "Saccammina limestone" of the North of England, the "Endothyra limestone" of North America, and the "Fusulina limestone" of Russia, all of which are of Carboniferous age. Of the Foram-

Fig. 6. — Section of Carboniferous limestone from Spergen Hill, Indiana, U.S., showing numerous large-sized *Foraminifera* (*Endothyra*) and a few oolitic grains, magnified. (Original.)

iniferal limestones of the Mesozoic period the most interesting and important is the White Chalk, the characters of which will be considered more fully later on. Lastly, in the Tertiary period there are various well-known Foraminiferal limestones, of which the most important and most widely distributed is the great calcareous deposit known as the "Nummulitic limestone."

Among Cœlenterate animals, the principal lime-makers are the true Corals (*Madreporaria*). Many of the limestones which enter into the composition of the crust of the earth, dating from the Ordovician period onwards, are more or less extensively composed of the skeletons of Corals. Though the Corals commonly occur in such a manner in the rock as to show clearly that they grew on the spot where the limestone was formed, it is questionable if any of the Palæozoic limestones can be properly said to be actual "coral-reefs," though some of the Devonian limestones of North America and Belgium may possibly be truly of this nature. In the Secondary and Tertiary periods, however, we meet with coralline limestones which may be considered as essentially similar in structure and mode of formation to the "coral-reefs" of the warm seas of the present epoch. The Corals, however, are not the only Cœlenterate animals which play an important part in the formation of limestones, for it is now known that certain of the *Hydrozoa* are likewise capable of giving rise to extensive calcareous deposits by the accumulation of their skeletons. Thus, certain of the Silurian and Devonian limestones are largely composed of the calcareous skeletons of the extinct *Hydrozoa* which constitute the group of the "Stromatoporoids." Other Palæozoic limestones are extensively made up of the remains of organisms like *Solenopora* and *Mitcheldeania*, which are possibly referable to the *Hydrozoa*. At the present day, the only *Hydrozoön* which is conspicuously concerned in the formation of limestone is the Hydrocoralline genus *Millepora*, which plays an important part in the construction of many of the existing "coral-reefs."

Of the *Echinodermata* there is only one order—viz., that of the Sea-lilies or *Crinoids*—which demands special mention in the present connection. At the present day, the Crinoids constitute a but feeble remnant of a once powerful and widely distributed group, and they are not known to exist anywhere in numbers sufficient to render them noteworthy as lime-makers. Among the older rocks of the earth's crust, however, and more particularly in deposits of Ordovician, Silurian, Devonian, and Carboniferous age, are found great beds of limestone, essentially composed of the broken stems and detached plates of Crinoids (fig. 7). Such limestones are known to geologists as "Crinoidal limestones" and "Encrinital marbles," and they are usually composed of more or less broken and rolled

fragments of Crinoids, showing that the materials of which they are composed had been subjected to the action of the sea before being consolidated into rock. In other cases, especially among some of the Crinoidal limestones of the Mesozoic period, the Crinoids seem to have grown on the spot where the limestone was deposited. Very generally, the Crinoidal fragments are sufficiently large and well preserved to be readily recognised, even with the unassisted eye; but even when they have been greatly abraded and worn down, their presence can usually be detected without difficulty by an examination of thin sections by means of the microscope. By this method it is, at any rate, almost always possible to determine whether or not a given fragment is Echinodermal, since the minute structure of the skeleton in the animals of this group is highly characteristic.

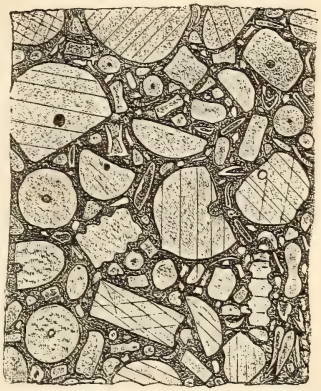


Fig. 7.—Section of Crinoidal limestone, from the Devonian (Hamilton Formation) of Canada, enlarged ten times. The matrix in which the Crinoidal fragments are enclosed, is mostly a fine calcareous mud. (Original.)

None of the members of the great series of the Annulose Animals can be said to play a very important part in the formation of limestones. Apart from the occasional presence in limestones of the calcareous cases of the Tubicolous Annelides, almost the only Annulose animals which ever contribute to lime-making are the *Crustacea*. In some cases, however, the calcareous crusts of certain groups of Crustaceans (particularly the Trilobites and the Ostracodes) constitute a noteworthy element in the composition of limestones.

On the other hand, the two existing groups of the Molluscoids—viz., the *Polyzoa* and the *Brachiopoda*, have both been extensively concerned in lime-making. In many of the Palæozoic limestones, the remains of *Polyzoa* constitute a conspicuous feature, though they cannot be said to form the bulk of the rock. In some of the Secondary and Tertiary limestones, however, the rock is really made up to a predominating extent of the calcareous skeletons of *Polyzoa*. Well-known examples of such so-called "Coralline limestones" are found in the Upper White Chalk of the continent of Europe, and in the "Coralline Crag" (Pliocene) of Suffolk and Norfolk. The Brachiopods, again, exerted their greatest activity as lime-makers during the Palæozoic period, many of the limestones of the Ordovician, Silurian, Devonian, and Carboniferous periods being

largely made up of the entire or fragmentary shells of animals belonging to this group.

Still more important are the true Molluscs, the shells of which have commonly been accumulated to form beds of limestone in all the great periods from the Ordovician onwards. Some of these "shell-limestones" are composed of the exuviæ of sedentary Molluscs, such as Oysters, and have therefore been formed in place. Excellent examples of such limestones are afforded by portions of the "Muschelkalk" of the Trias of Germany, and the massive "Hippurite limestone" of southern Europe. In other cases, the limestone is made up principally of the broken fragments of Molluscan shells which have been subjected to the transporting and abrading action of the sea; and the rock has therefore been formed in a manner similar to that in which the "shell-sand" of modern shores has been produced. In still other cases, again, the limestone has been formed by the slow accumulation on the sea-bottom of the shells of "pelagic" Molluscs, which live at or near the surface of the sea, and the skeletons of which fall to the bottom on the death of their owners. Of this nature are the "Pteropodal ooze" of the present period and the "Pteropodal limestones" associated with

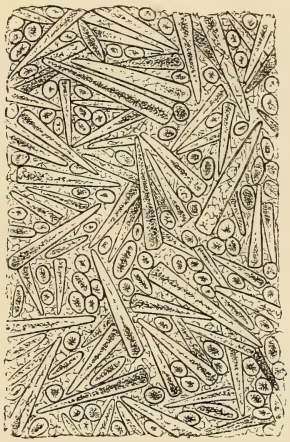


Fig. 8.—Section of a Pteropodal limestone, made up of the shells of *Styliola fissurella*, Hall, from the Devonian (Genesee Slates), Canandaigua, United States. Enlarged twenty times. (Original.)

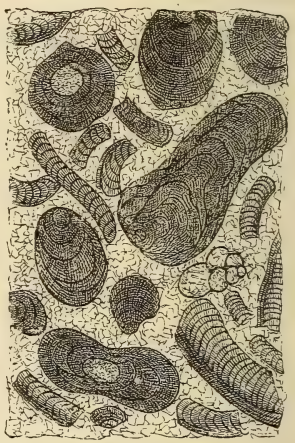


Fig. 9.—Section of a Tertiary limestone ("Leitha-kalk"), from Nussdorf, near Vienna, composed almost entirely of fragments of Nullipores cemented together by a crystalline matrix. Enlarged three times. (Original.)

uplifted coral-reefs. Similar "Pteropodal limestones" are known to occur even in deposits as old as the Devonian (fig. 8), but they are of rare occurrence and are usually of small thickness. Lastly, it is to be noticed that limestones may be formed as well by fresh-

water Molluscs as by those which inhabit the sea. The recent "shell-marls" are examples of deposits of this nature, and various Tertiary and Secondary limestones are more or less extensively charged with the shells of fresh-water Gastropods and Bivalves.

Finally, it is to be noted that animals are not the exclusive agents concerned in the building up of limestones. Certain of the calcareous Algæ—such as the "Corallines," the "Nullipores," and the singular family of the *Dactyloporidæ*—are capable, singly or in combination with other organisms, of forming accumulations of lime, sometimes upon a most extensive scale. The two latter groups, in particular, have given rise to vast masses of limestone. Examples of the *Dactyloporidæ* occur even in the Palæozoic limestones, but the most famous and most extensive deposit formed by *Algæ* of this group is the well-known "Gyroporella-limestone" of the Bavarian and Tyrolese Alps, the age of which is Triassic. Limestones formed more or less largely of "Nullipores" (*Lithothamnion*) occur to some extent in the Secondary rocks, and are extensively developed in the Tertiary series. The most famous of these is the "Nulliporen-kalk" or "Leitha-kalk" of the Vienna basin (fig. 9), which attains a considerable thickness, and extends from Austria, through the Balkans, to Asia Minor and Persia.

In connection with the subject of the constitution of the ordinary organic limestones, the researches of Dr Sorby on the precise chemical composition of calcareous organisms demand a brief notice. The carbonate of lime in calcareous organisms exists sometimes in the condition of *aragonite*, sometimes in that of *calcite*. The chief differences between these two allotropic conditions of calcium carbonate are: (1) that calcite is optically uniaxial, whereas aragonite is biaxial; (2) that calcite has a specific gravity of about 2.72, whereas the density of aragonite is 2.93; and (3) that aragonite is harder than calcite, as shown by the fact that the former will scratch a crystal of Iceland spar along the line of the short diagonal of one of the crystalline facets, whereas the latter will not do so. In the second place, the composition of the skeleton of calcareous organisms varies in different groups, some having a skeleton wholly of calcite and others wholly of aragonite, while in some cases the skeleton is composed in part of calcite and in part of aragonite. The following table shows the principal variations in this respect, as determined by the researches of Sorby:—

1. *Foraminifera.*—The test of the calcareous *Foraminifera* appears to be in general composed of calcite, though a certain amount of aragonite seems to be sometimes present. [In the porcellanous *Foraminifera* the test is very probably wholly composed of aragonite.]

2. *Madreporaria.*—The true Corals have the skeleton composed, mainly or wholly, of aragonite.

3. *Alcyonaria.*—The skeleton of the Alcyonarian Corals is mainly of calcite, but with indications of the presence of a small amount of aragonite or phosphate of lime.

4. *Echinodermata.*—The skeleton is always composed essentially of calcite.

5. *Annelida.*—The skeleton seems to be always composed of calcite.

6. *Crustacea.*—The shell of the Crustaceans is mainly composed of calcite, with a variable intermixture of phosphate of lime.

7. *Polyzoa.*—The skeleton of the calcareous *Polyzoa* consists of a variable intermixture of calcite and aragonite, the two inseparably blended together.

8. *Brachiopoda.*—The shell appears to be always composed of calcite [sometimes with a considerable proportion of phosphate of lime].

9. *Lamellibranchiata.*—The shell of the Bivalve Molluscs is often composed wholly of aragonite, but in other cases (*e.g.*, Oysters and Scallops) it is wholly of calcite, while in others (*e.g.*, in Mussels, *Pinna*, &c.) the shell has an outer layer of calcite and an inner layer of aragonite.

10. *Gastropoda.*—Most Univalve Molluscs have the shell wholly composed of aragonite, but some (such as *Patella*, *Fusus*, *Littorina*, and *Purpura*) possess an outer layer of calcite and an inner layer of aragonite.

11. *Cephalopoda.*—The shells of Cephalopods appear to be mainly composed of aragonite.

The above-mentioned variations in the chemical composition of the skeleton of calcareous organisms have been shown by Sorby to be associated with important differences as to the condition of preservation of these skeletons as fossils. It has been shown, namely, that aragonite is relatively much less *stable* than calcite. Calcite has no tendency, under any natural circumstances, to pass into the condition of aragonite; aragonite very readily passes into the condition of calcite. Hence in the processes connected with fossilisation, calcareous skeletons composed of aragonite are much more liable to undergo alteration, replacement, or even dissolution, than are those composed of the more stable calcite. It is for this reason that the shells of Gastropods and Lamellibranchs—which are commonly composed entirely of aragonite—are so often found as fossils in the condition of mere "casts," the original shell having been wholly removed by solution, or having been replaced by a pseudomorph composed of irregularly placed (unoriented) crystals of calcite. For the same reason, in cases where the shell consists in part of aragonite and in part of calcite, it is common for the aragonite layer to have been removed, while the calcite layer has been preserved.

Before leaving the subject of limestones, it may be advisable to notice briefly the more important differences as regards chemical constitution or minute structure which give rise to special types of limestone, and which not infrequently have a palæontological significance. The differences here specially alluded to may be considered under the following heads:—

(1.) *Lithological Nature.*—Many of the differences which distinguish particular varieties of limestone concern simply the mineral nature of the rock, and are of no special importance from a palæontological point of view. Thus, many limestones are more or less extensively made up of angular quartz-grains embedded in a matrix of crystalline calcite (fig. 2, B), the rock becoming an *arenaceous* limestone. There are innumerable links, in fact, between what may be called a "calcareous sandstone" and a true "limestone" containing

a small number of scattered grains of quartz. In other cases more or less silicate of alumina is present, and the rock becomes an *argillaceous* limestone, passing, in extreme cases, into a "calcareous shale." In other cases, again, the limestone may be more or less highly charged with minute particles of carbon, or may be more or less impregnated with certain hydrocarbons, the rock becoming a *carbonaceous* limestone or a *bituminous* limestone, as the case may be. The term "marble" is one of no very precise signification, any limestone which is sufficiently hard and compact to take a high polish being usually spoken of under this name. "Chalk," again, from a purely lithological point of view, is a soft pulverulent limestone, but it is occasionally quite hard and compact; and its truly essential characters depend upon its organic structure, which will be more fully considered later on.

(2.) *Chemical Constitution.*—The most important variation in limestones, from a chemical point of view, is established by the presence in the rock of more or less carbonate of magnesia. The presence of a certain amount of magnesia in a limestone is a very common phenomenon, and often only admits of detection by means of chemical analysis. Limestones which contain a variable and comparatively small amount of carbonate of magnesia are spoken of as "magnesian limestones," and they often differ little or not at all from ordinary limestones in either appearance or structure. Where there is a notable proportion of carbonate of magnesia present, the limestone often assumes a brownish or yellowish colour, with a sandy aspect, while it shows a marked tendency to undergo secondary crystallisation. This is shown in some cases by the development of a concretionary structure in the rock, the so-called "concretions" being truly the result of an imperfect form of crystallisation. Thin sections, also, of such magnesian limestones invariably show that the rock has undergone more or less extensive recrystallisation, subsequent to consolidation; and the organic fragments originally present in the rock have been thereby more or less largely obscured, or, it may be, completely obliterated. Owing, further, to the comparative insolubility in water of carbonate of magnesia as compared with carbonate of lime, the larger calcareous organisms (such as the shells of Molluscs) in the more highly magnesian limestones have been commonly dissolved out of the rock, and are now only represented by casts and moulds. Where the carbonate of magnesia is present in a limestone in such quantity as to form with the carbonate of lime a true double carbonate, the rock is what is strictly called a "dolomite." The true dolomites, when examined microscopically, are always found to be more or less intensely crystalline. In some cases the recrystallisation to which the rock has been subjected subsequent to its original formation has not been

sufficient to absolutely destroy any organic remains present in the rock. Thus, in the dolomites of the Guelph formation (Silurian) of Canada, the presence of fossils can commonly be recognised in thin sections, though these have always undergone more or less secondary change, and have usually been replaced by calcite or by peroxide of iron, or are represented simply by vacant spaces in the rock. On the other hand, in many dolomites (fig. 10) secondary crystallisation has been as complete as in statuary marble, and any organic remains which may have existed in the rock to begin with have been totally obliterated.

With regard to the origin of magnesian limestones, it is sufficient here to say that those in which magnesia is present in comparatively small quantity probably owe their peculiarities to the conditions under which they were originally deposited; and there are even true dolomites in which there is ground for thinking that the rock was

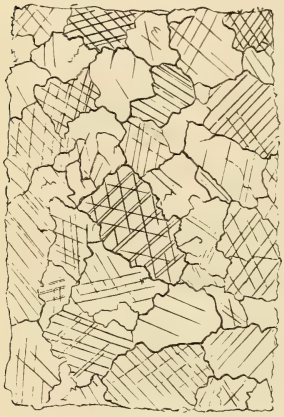


Fig. 10.—Thin section of dolomite, from Sweden, enlarged ten times. The rock is an aggregate of comparatively large crystals, which exhibit the characteristic cleavage-lines of carbonate of lime. (Original.)

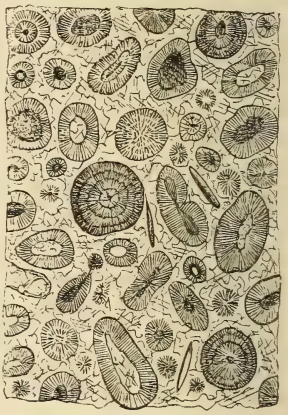


Fig. 11.—Section of oolitic limestone, Carboniferous, Kershope Foot, enlarged thirty times. Some of the spheroids have no definite boundaries, and consist simply of diffuse radiating crystallisations. (Original.)

magnesian from the first. In other cases, again, it cannot be doubted that the rock was originally a normal limestone, and that "dolomitisation" was the result of secondary changes affecting the rock subsequent to its original formation.

(3.) *Minute Structure.*—The most important of the ordinary structural peculiarities of limestones is what is known as the "*oolitic*" structure. The subject of the oolitic structure of calcareous rocks is one of great complexity, and the morphological differences which exist between different oolites are very numerous and highly remark-

able. It will not, therefore, be possible here to do more than glance at some of the more salient peculiarities presented by oolitic limestones. If a thin slice of any ordinary oolitic limestone be examined under the microscope, it will be found to exhibit more or less numerous rounded or oval grains, of variable size, embedded in a matrix of crystalline calcite (fig. 11). Each oolitic grain, or spheroid, ordinarily exhibits a more or less obvious structure out of concentrically superimposed layers, each layer being composed of minute crystals of calcite arranged in a radiating manner, with their long axes perpendicular to the surface. Very commonly there may be detected in the centre of the grain a larger or smaller foreign body, such as a grain of quartz or a fragment of some calcareous organism, which has served as a nucleus round which the spheroid has been built up. In other cases, no traces of a foreign nucleus can be recognised. According to the view usually entertained, oolitic grains of the type just described have been produced by "the original deposition of calcite round nuclei gently drifted along by currents of the ordinary temperature, which caught up more or less of the surrounding mechanical impurities" (Sorby). According to this view, therefore, the rock was primitively a loosely compacted aggregate of oolitic grains, along with entire or fragmentary calcareous organisms, and solidification was a secondary process, due to the percolation through the mass of water charged with carbonate of lime in solution, and the consequent precipitation of crystalline calcite in all the vacant spaces between the grains. This view, doubtless, affords an adequate explanation of the formation of the ordinary oolitic limestones. There are, however, cases in which it would rather seem that the formation of the oolitic grains has been due to secondary crystallisation in an originally normal limestone. Thus, in certain limestones some of the oolitic grains have no definite boundaries, but consist simply of diffuse radiate crystallisations, which may or may not have a central nucleus for their starting-point (fig. 11). The structure just alluded to must, however, be carefully distinguished from cases in which the oolitic grains have undergone recrystallisation at some period posterior to their original formation. In this latter case, the grains preserve their outlines, but the primitive radiate and concentric structure is more or less completely destroyed, and the spheroids consist simply of irregularly placed crystals of comparatively large size.

In all the fossiliferous formations, from the Ordovician onwards, oolitic limestones are of common occurrence; but they vary considerably in their more minute characters. In one of the commonest varieties of oolitic limestones the grains assume a greatly elongated form, when the name of "spheroids" is hardly applicable to them. Such elongated grains have been sometimes regarded as owing their

shape to pressure, but it does not appear that this is an adequate explanation, and their mode of origin is still obscure.

(4.) *Superinduced Structure.*—There are probably no limestones, including even those now actually in process of formation, which are absolutely free from superinduced structural peculiarities of one kind or another. In a general way, these superinduced peculiarities depend upon a more or less extensive recrystallisation of portions of the rock, it being sometimes the matrix of the limestone which is thus affected, sometimes the included fragments, and sometimes both. In many cases, the secondary crystallisation of a limestone may be the result of slow chemical or physical changes, connected in the main with the percolation through the rock of water holding carbonic acid or other ingredients in solution. As regards the organic fragments present in most limestones, these gradual changes are doubtless much facilitated by the readiness with which aragonite passes into the condition of calcite. As a general rule, however, these slow alterations do not affect the structure of the limestone so profoundly but that the original constitution of the rock is easily recognisable by suitable methods of examination. In many cases, on the other hand, and especially among the older limestones of the earth's crust, the rock has undergone changes of a much deeper and more far-reaching character than those above alluded to. The most prominent of these changes consists in a more or less complete crystallisation of the rock, leading to a more or less complete obliteration of any fossils which it may have contained. The general causes which contribute to bring about this thorough crystallisation of limestones are heat and pressure, singly or together, combined with the action of percolating water, which is rendered chemically potent by having certain substances dissolved in it.

That the application of a powerful heat to limestone will cause its crystallisation is sufficiently exemplified by the well-known phenomena observable in a limestone when intersected by an intrusive igneous rock. Thus, limestone in the immediate neighbourhood of a trap-dyke or a mass of granite is found to have been converted into a crystalline marble, in which, as a rule, no traces of organic structure can be detected under the microscope. When developed upon a larger scale, crystalline limestones are usually found in regions which can be shown to have been subjected to powerful earth-movements, one result of which must have been the application to the rocks of the region of intense pressure. Usually greater or less elevation of temperature has co-operated with the pressure in producing alterations in the structure of the rocks affected by these movements. Speaking generally, therefore, we may regard the "regional" crystallisation of limestones as due to the application of great pressure to deeply buried masses of these rocks, raised to a

moderately high temperature and impregnated with water holding more or less powerful chemical agents in solution.

The initial stages of the changes above alluded to can be well observed in many of the older limestones, where the rock has been subjected to sufficient pressure to produce crushing and cleavage, but where crystallisation has been imperfectly or not at all induced. Some of such limestones show plain signs of intense pressure in the distortion and partial destruction of their contained organic fragments, as seen in microscopic sections, at the same time that the mass of the rock has remained free from crystallisation. In other cases, as in some of the Devonian limestones of Devonshire, not only are the organic remains in the rock more or less distorted by pressure, but they have usually undergone recrystallisation, though this has not been sufficiently intense to render them unrecognisable. The complete development of the changes here in question is seen in statuary marble and in the "metamorphic" limestones generally, where a microscopic examination of the rock shows it to be a mere aggregate of variously-sized crystals of carbonate of lime (or, in the case of dolomites, of the double carbonate of lime and magnesia), all traces of organic structure being entirely obliterated (fig. 10). In some instances (as, for example, in the case of the white statuary marble of Carrara) it can be shown that such a purely crystalline limestone was, to begin with, a quite normal limestone, which was in part caught up in the folds of a mountain-chain, and thus subjected locally to enormous pressure. In other cases, we have evidence that a whole region has been subjected to powerful earth-movements, the pressure evolved in which has been so intense and so widely diffused that no part of the original limestone has preserved its primary organic structure. In such cases—as, for example, in the crystalline limestones of the Highlands—adventitious minerals, such as serpentine, are commonly developed in the rock, showing that active chemical changes have accompanied the mechanical pressure to which the rock has been subjected. We must not, however, lose sight of the possibility that the "metamorphic" limestones of the Archæan period (such as the Laurentian limestones of Canada) *may* owe their crystalline character and their mineral peculiarities, not to alteration subsequent to deposition, but to the conditions under which they were originally formed. It is also to be remembered that in some cases we meet with beds of granular and crystalline limestone intercalated in a series of more or less completely normal limestones, without there being any obvious reason for the difference. In such cases, it is probable that the entire series of deposits has been subjected to pressure, and that, owing to slight peculiarities in mineral or chemical constitution, certain bands have undergone crystallisation, while others have escaped with nothing more than a certain

degree of induration. Indeed, even in a single hand-specimen, it is not unusual to find that some portions of the rock have undergone complete secondary crystallisation, while others are comparatively unchanged.

Siliceous Organic Rocks.—We have seen that the *calcareous* or lime-containing rocks are the most important group of organic deposits, while the *siliceous* or flint-containing rocks may be regarded as the most important, most typical, and most generally distributed of the mechanically formed deposits. We have, however, now briefly to consider certain deposits which are more or less completely formed of flint, but which nevertheless are essentially organic in their origin.

Silica is probably invariably held in solution in small quantity in natural waters, whether these be fresh or salt. Small as is the quantity of silica dissolved by rivers or by the sea, there is sufficient of it to supply material for the flinty skeletons of innumerable organisms, both animal and vegetable; and the accumulation of such skeletons may, under favourable conditions, give rise to very considerable deposits of siliceous matter. The two principal groups of animals which secrete a siliceous skeleton, and may thus produce deposits of silica, are certain forms of the Sponges and the minute organisms known as the *Polycystina*. In a very large number of Sponges, the skeleton consists of variously shaped needles or "spicules" of flint, sometimes detached and entirely separate, at other times more or less closely united with one another. The accumulation of these spicules at the bottom of the sea may give rise to extensive siliceous deposits, such as have been described by Dr Hinde as occurring in the Lower and Upper Greensand of Britain. In some cases the skeletal structures of Sponges which have been accumulated to form deposits such as those above alluded to, have undergone comparatively little change, and their presence can be readily recognised. In other cases, however, these siliceous structures have undergone much alteration, and their existence cannot be demonstrated without difficulty. It is known, namely, that there is a marked difference as regards relative solubility in water between ordinary crystalline *quartz*, on the one hand, and the peculiar form of silica which occurs in the skeletons of animals and plants, on the other hand. Quartz is relatively a very stable substance, and it is only in highly heated waters, containing in solution such ingredients as the alkaline carbonates (as, for example, in the waters of certain hot springs), that quartz is ever found to be dissolved in large quantity. On the other hand, the silica which forms the skeleton of flint-secreting animals and plants exists under a peculiar modification —as "amorphous" or "colloidal" silica—which is comparatively unstable, and, under suitable conditions, freely soluble in water. Hence, siliceous deposits formed by the accumulation of the flinty

skeletons of animals and plants are very liable to be affected by secondary changes, chiefly due to the percolation of water throughout their mass. As the main result of these changes, the siliceous skeletons become more or less extensively dissolved, the percolating water becoming thus charged with a larger or smaller amount of silica in solution. This dissolved silica is ultimately redeposited in the solid form, having, however, now lost its organic structure. By this partial solution of the skeletons of siliceous organisms, and the subsequent precipitation of the dissolved silica thus obtained, we may explain the common presence of nodules or beds of "flint" or "chert" in many of the great geological formations. This subject will, however, be treated of in greater detail in connection with the palæontological history of the Sponges.

The *Polycystina* are minute organisms belonging to the *Protozoa*, and nearly related to the *Foraminifera*, from which they differ, among other characters, by the fact that they secrete a "test" or skeleton of flint instead of one composed of lime. The *Polycystina* have a wide distribution in our present seas, and their skeletons are very generally recognisable, in greater or less numbers, in the deep-sea muds of the great oceans, being easily recognised by their exquisite shape, their glassy transparency, the general presence of longer or shorter spines, and the sieve-like perforations in their walls. In many places, in fact, especially in the colder portions of the great oceans, or at very great depths, the "Globigerina ooze" disappears, and its place is taken by a "Radiolarian ooze" composed almost wholly of the shells of *Polycystina*. Similar deposits, made up of the flinty skeletons of these Radiolarians, have been formed at previous periods of the earth's history, and now form part of the earth's crust. The two most famous of these deposits occur in Barbados and in the Nicobar Islands, the former being well known to workers with the microscope as the "Barbados earth" (fig. 12).

In addition to flint-producing animals, we have also the great group of fresh-water and marine microscopic plants known as *Diatoms*, which likewise secrete a siliceous skeleton, often of great beauty. The skeletons of Diatoms are found abundantly at the present day in lake-deposits, guano, the silt of estuaries, and in the mud which covers many parts of the sea-bottom; they have been detected in strata of great age; and in spite of their microscopic dimensions, they have not uncommonly accumulated to form deposits of great thickness, and of considerable superficial extent. Thus the celebrated deposit of "tripoli" ("Polir-schiefer") of Bohemia, largely worked as polishing-powder, is composed wholly, or almost wholly, of the flinty cases of Diatoms, of which it is calculated that no less than forty-one thousand millions go to make up a single cubic inch of stone. Another celebrated deposit is the so-

called "Infusorial earth" of Richmond in Virginia (fig. 13), where there is a stratum, in places thirty feet thick, composed almost entirely of the microscopic shells of Diatoms.

In addition to deposits formed of flint itself, there are other siliceous deposits formed by certain *silicates*, and also of organic

Fig. 12. — Shells of *Polycystina* from "Barbados earth"; greatly magnified. (Original.)

Fig. 13.—Cases of Diatoms in the Richmond "Infusorial earth"; highly magnified. (Original.)

origin. It has been shown, namely—by observations carried out in our present seas—that the shells of *Foraminifera* are liable to become completely infiltrated by silicates (such as "glauconite," or silicate of iron and potash). Should the actual calcareous shell become dissolved away subsequent to this infiltration—as is also liable to occur—then, in place of the shells of the *Foraminifera*, we get a corresponding number of green sandy grains of glauconite, each grain being the *cast* of a single shell. It has thus been shown by Dr W. B. Carpenter that the green sand found covering the sea-bottom in certain localities (as found by the Challenger expedition along the line of the Agulhas current) is really organic, and is composed of casts of the shells of *Foraminifera*. Long before these observations had been made, it had been shown by Professor Ehrenberg that the green sands of various geological formations are often composed in part of the internal casts of the shells of *Foraminifera;* and we have thus another and a very interesting example how rock-deposits of considerable extent and of geological importance can be built up by the operation of the minutest living beings.

Carbonaceous Deposits.—It only remains in connection with the general subject of the organically formed rocks to shortly consider the rock-deposits in which *carbon* is found to be present in greater or less quantity. In the great majority of cases where rocks are found to contain carbon or carbonaceous matter, it can be stated with certainty that this substance is of organic origin, though it is

not necessarily derived from vegetables. Carbon derived from the decomposition of animal bodies is not uncommon; though it never occurs in such quantity from this source as it may do when it is derived from plants. Thus, many limestones are more or less highly bituminous; the celebrated siliceous flags or so-called "bituminous schists" of Caithness are impregnated with oily matter apparently derived from the decomposition of the numerous fishes embedded in them; Silurian shales containing Graptolites, but destitute of plants, are not uncommonly "anthracitic," and contain a small percentage of carbon derived from the decay of these zoophytes; whilst the petroleum so largely worked in North America has not improbably an animal origin. That the fatty compounds present in animal bodies should more or less extensively impregnate fossiliferous rock-masses, is only what might be expected; but the great bulk of the carbon which exists stored up in the earth's crust is derived from plants; and the form in which it principally presents itself is that of *coal*. We shall have to speak again, and at greater length, of coal, and it is sufficient to say here that all the true coals, anthracites, and lignites, are of organic origin, and consist principally of the remains of plants in a more or less altered condition. The bituminous shales which are found so commonly associated with beds of coal, also derive their carbon primarily from plants; and the same is certainly, or probably, the case with similar shales which are known to occur in formations younger than the Carboniferous. Lastly, carbon may occur as a conspicuous constituent of rock-masses in the form of *graphite* or *black-lead*. In this form it occurs in the shape of detached scales, or of veins or strings, or sometimes of regular layers; and there can be little doubt that in some instances it has an organic origin, though this is not capable of direct proof. When present, at any rate, in quantity, and in the form of layers associated with stratified rocks, as is sometimes the case in the Laurentian formation, there seems to be considerable probability in the hypothesis which would regard it as primarily of organic origin and as of the nature of an altered coal.

CHAPTER III.

SUCCESSION OF FORMATIONS—CONTEMPORANEITY OF STRATA—GEOLOGICAL CONTINUITY.

Different Ages of the Aqueous Rocks.

The two principal tests by which the age of any particular bed, or group of beds, may be determined, are superposition and organic remains—a third test being sometimes afforded by mineral characters. The first and most obvious test of the age of any aqueous rock is its relative position to other rocks. Any bed or set of beds of sedimentary origin is obviously and necessarily older than all the strata which surmount it, and younger than all those upon which it rests. It is to be remembered, however, that superposition can at best give us but the *relative* age of a bed as compared with other beds of the same region. It cannot give us the *absolute* age of any bed; and if we are ignorant of the age of any of the beds with which we may be dealing, we have to appeal to other tests to learn more than the mere order of succession in the particular region under examination. Moreover, deposits formed in isolated basins, and not in an area of continuous sedimentation, have necessarily no stratigraphical relations to deposits laid down in other areas, and their age can only be determined by palæontological tests. This difficulty, as pointed out by Professor C. A. White, is enhanced when such isolated sediments have been produced within inland *fresh* waters; since such sediments, from their mode of formation, can have no place in any observed order of superposition of *marine* deposits, and would, in addition, necessarily contain wholly different fossils as compared with beds laid down in the sea.

The second, and in the long-run more valuable, test of the age of the different sedimentary beds, is that afforded by their organic remains. Still, this test is also by no means universally applicable, nor in all cases absolutely conclusive. Many aqueous rocks are unfossiliferous through a thickness of hundreds, or even thousands,

of feet of little altered sediments; and even amongst beds which do contain fossils, we often meet with strata of a few feet or yards in thickness, which are wholly destitute of any traces of life. Many fossils, again, range vertically through many groups of strata, and in some cases even through several formations. Such fossils, therefore, if occurring by themselves, or considered apart from other associated organisms, are not conclusive as to the age of any particular set of beds. As the result, however, of combined palæontological and geological researches, it is now possible for us to divide the entire series of stratified deposits in any given region into a number of definite rock-groups or formations, each of which is characterised by possessing an assemblage of organic remains which do not occur in association in any other formation. Such an assemblage of fossils, characteristic of any given formation, represents the *life* of the particular period in which the formation was deposited. It follows from this, that whenever we can get a group or collection of fossils from any particular bed or set of beds, there is rarely any difficulty in determining, as regards the particular region under examination, the precise geological horizon of the beds in which the fossils occur.

With certain limitations, however, we may go much further than this. Not only are the great formations characterised by special and characteristic assemblages of animals and plants; but, in a general way, each subdivision of each formation has its own peculiar fossils, by which it may be recognised by a skilled worker in palæontology. Whenever, for instance, we meet in Britain with the fossils known as Graptolites, we may be sure that we are dealing with Cambrian, Ordovician, or Silurian rocks. We may, however, go much further than this. If the Graptolites belong to certain genera, we may be sure that we are dealing with Ordovician rocks. Furthermore, if certain special forms are present, we may be even able to say to what exact part or subdivision of the Ordovician series they belong.

All these conclusions, however, would have to be accompanied by a tacit but well-understood reservation. No Graptolites have ever been found in Britain out of rocks known upon other grounds to belong to one or other of the three formations above mentioned; but there is no reason why they might not at any time be found in younger deposits. In the same way, the species and genera which we now regard as characteristic of the Ordovician, might at any time be found to have survived into the Silurian period. We should never forget, therefore, in determining the age of a rock by palæontological evidence only, that we are always reasoning upon generalisations which are the result of experience alone, and which may at any time be overthrown by fresh discoveries.

There is, moreover, another important principle to take into

account in considering the value of fossils as tests of the age of strata. Within a given area of such dimensions that we may suppose it to have formed a single life-province, we shall undoubtedly find that there is a recognisable succession of life-forms, so that particular groups of rocks may be safely assigned, on the strength of their contained fossils, to fixed places in the geological series, and a definite chronological succession of the strata may thus be established *for the region examined.* When we come, however, to compare together the successive life-forms of widely remote areas, which must be supposed to have always belonged to different life-provinces, we cannot expect to find anything like a *precise* identity. We shall probably be able to establish a *general* correspondence or analogy, sufficient to establish a general parallelism of the successive groups of strata in the two regions compared; but it can only be in exceptional circumstances that the fauna of a particular series of beds in one region can possibly be largely identical with that of a coeval series in a widely distant region. This principle is sufficiently established by the simple consideration that the assemblages of animals now existing simultaneously in different regions are so unlike each other that we can by their means divide the earth's surface into a number of definitely bounded "zoological provinces," and that there is every reason to suppose that similar life-provinces have existed in all the great geological periods of which the palæontological history has been preserved. If, on the other hand, we were to find that the rocks deposited in any particular period of the earth's history contained absolutely identical fossils in all parts of the world, we should be forced to conclude that during that period there were no "zoological provinces" developed, but that the entire terrestrial surface constituted a single vast life-province inhabited by the same kinds of animals and plants. Nothing that we have of actual evidence, derived either from the past or the present, would, however, support such a supposition; but this point will be more clearly brought out in dealing with the "contemporaneity" of strata in different regions.

General Chronological Succession of the Stratified Rocks.

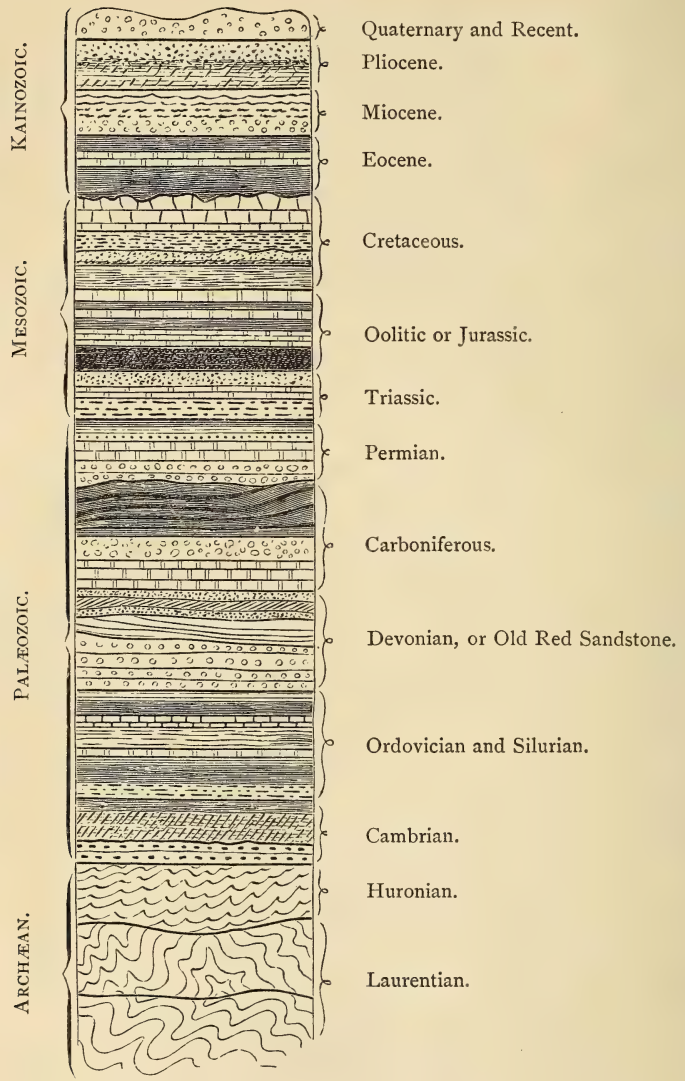
As the result of observations made upon the superposition of rocks in different regions, from their mineral characters, and from their included fossils, geologists have been able to divide the series of the stratified rocks into a number of different divisions or "rock-systems," each characterised, in any given region, by a *general* uniformity of mineral composition and by a special and peculiar *assemblage of life-forms*, and each representing a "period" in the earth's history. In every country in the world that has been geo-

logically investigated, such a chronological succession of the stratified rocks has been established, but the order of succession is not necessarily identical even in regions geographically close together. On the contrary, as above pointed out, a comparison of the succession of the stratified deposits in two regions widely remote from one another in space will show that, though a general parallelism will exist, the corresponding rock-groups in the two regions will not contain absolutely identical fossils, and that certain rock-groups which are present in one region are absent in the other. In no one region, therefore, do we meet with an absolutely complete and continuous succession of stratified rock-groups, nor could such ever have been laid down except in a region which had been continuously beneath the sea and constantly the seat of sedimentation since the beginning of geological time. At all times of which we have geological record, the earth's surface has, however, consisted partly of dry land and partly of sea, and the terrestrial and marine areas have simply undergone displacement and have been changed in position from time to time. During each successive epoch, therefore, certain areas have been the seat of sedimentation, while others have been dry land; but the dry land of one period may become the sea of the next, and *vice versâ*, and sedimentation is thus transferred in the course of ages from one place to another. Hence when we meet with a stratified deposit in one region (A) which has no representative in an adjoining region (B), we know that one or other of two things has occurred. In the first place, B may have been dry land while A was beneath the ocean. In that case, the missing deposit was never laid down in B at all. Or, in the second place, both of the areas may have been under the sea simultaneously, and the deposit in question may have been originally laid down in both; but A may have remained continuously under water, while B may have been elevated to form dry land, undergoing in process of elevation sufficient denudation to destroy the deposit in question.

By a comparison of many different areas, geologists have been enabled to frame a *general order of succession of the stratified rocks*, which, though based originally upon the facts observed in Europe, is nevertheless, *in its main outlines*, applicable to other and widely distant regions. This general succession is diagrammatically shown in the annexed ideal section of the crust of the earth. The most ancient of all the stratified rocks are more or less intensely crystalline in character, and no undoubted fossils have hitherto been detected in them. They are grouped together under the general name of the *Archæan* rocks, and comprise several rock-systems, of which the best established is the Laurentian series of North America and of Europe. All the rock-groups above the Archæan are more or less richly fossiliferous, and are divided into three main "groups," each com-

IDEAL SECTION OF THE CRUST OF THE EARTH.

FIG. 14.



prising several smaller divisions or "systems." The oldest group comprises the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian "systems," which are spoken of as the *Primary*

or *Palæozoic* rocks (Gr. *palaios*, ancient; *zoe*, life), because of the wide divergence of their animals and plants from any now existing upon the globe. The Triassic, Jurassic, and Cretaceous systems are grouped together as the *Secondary* or *Mesozoic* formations (Gr. *mesos*, intermediate; *zoe*, life), because their organic remains are intermediate between those of the Palæozoic period, and those of more modern strata. The Eocene, Miocene, Pliocene, and Pleistocene rocks are grouped together under the head of *Tertiary* or *Kainozoic* rocks (Gr. *kainos*, new; *zoe*, life), because the fossil animals and plants which they contain approximate in character to those now existing upon the globe.

According to the recommendations of the International Geological Congress, the following names should be employed for the larger and smaller divisions of the stratified rocks and the time-divisions to which these correspond, the terms being arranged in order of their comprehensiveness.

Divisions of sedimentary formations ("*terranes*").	*Corresponding chronological terms.*
Group.	Era.
System.	Period.
Series (or *Section*).	Epoch.
Stage (or *Beds*).	Age.

The term "formation," very commonly employed by British geologists, is perhaps best retained as a loose general term to indicate any set of beds, large or small, which have some common characteristic, either as to mineral nature or fossil contents, or as to the mode in which the deposit has been formed. If used in a *definite* sense, it should be employed with reference to the mode of formation or the lithological nature of the rocks; so that we may suitably speak of the "Chalk Formation," or the "Coal Formation," or of a "marine formation," or a "lacustrine formation."

The following table exhibits the great geological "systems," as developed in Europe, in chronological order, beginning with the youngest, the more important and typical British representatives of each being likewise mentioned :—

General Classification of Post-Archæan Fossiliferous Deposits.

Kainozoic or Tertiary Group.	1. Recent Formations.—Deposits now in process of formation in seas, rivers, and lakes, and on land, such as the sands and muds of shallow seas, modern calcareous deposits like shell-beds, coral-reefs, &c., deep-sea muds, shell-marls, river-gravels, peat-mosses, &c.
	2. Quaternary or Pleistocene Formations.—Post-glacial, Glacial, and Pre-glacial deposits, in which the Molluscs belong to existing species, but some of the Mammals are referable to extinct forms. Often grouped with the preceding under the general name of the "Post-tertiary deposits."

Kainozoic or Tertiary Group.

3. Pliocene System.—(British representatives, the Norwich Crag, and the Red and White Crags of Suffolk.)
4. Miocene System.—(The Upper Miocene or "Falunian" series and the Middle Miocene or "Mayencian" series are wanting or doubtfully represented in Britain. The Lower Miocene series is often grouped with the Upper Eocene series as a separate system, under the name of *Oligocene*, represented in Britain by the Hempstead, Bembridge, Osborne, and Headon beds.)
5. Eocene System.—(British representatives, the Barton Clay, Bagshot and Bracklesham beds, London Clay, Thanet Sands, &c.)

Mesozoic or Secondary Group.

6. Cretaceous System.—(British representatives, the Chalk, the Upper Greensand, the Gault, the Lower Greensand, and the Wealden Clays and Hastings Sand. The Lower Greensand and Wealden series are commonly grouped together as the "Neocomian" series.)
7. Jurassic System.—(British representatives, the Purbeck beds, Portland beds, Kimeridge Clay, Coral Rag, Oxford Clay, Cornbrash and Forest Marble, Great Oolite, Stonesfield Slate, Fuller's Earth, Inferior Oolite, and Lias.)
8. Triassic System.—(The uppermost Triassic or "Rhætic" beds are feebly represented in Britain by the Penarth beds and White Lias, and the "Keuper" and "Bunter Sandstein" of the continent of Europe have corresponding British representatives. The great marine division of the "Muschelkalk," which is largely represented in the Trias of Germany, is not developed in Britain.)

Palæozoic Group.

9. Dyas or Permian System.—(The deposits included under this name are more extensively developed in the European area than they are known to be in any other region, and it is doubtful if they can be regarded as a distinct "system." The chief British representatives of the Permian rocks are the Marl-slate and Magnesian Limestone, or "Zechstein," and the Penrith Sandstones or "Rothtodtliegendes.")
10. Carboniferous System.—(British representatives, the Coal-measures, the Millstone Grit series; the Yoredale series, the Scar-limestone series, and the Tuedian or Cement-limestone series.)
11. Devonian System.—(The Devonian rocks of Devonshire are marine, and contain representatives of the Lower, Middle, and Upper Devonian of the continent of Europe. The Old Red Sandstone of Scotland and of South-Western England and Wales was perhaps deposited in inland waters.)
12. Silurian System.—(British representatives, the Ludlow series, Wenlock series, and May Hill series.)
13. Ordovician System.—(British representatives, the Bala series, the Llandeilo series, and the Arenig series.)
14. Cambrian System.—(British representatives, the Tremadoc series, the Lingula Flag series, the Menevian series, and the Harlech series.)

Palæontological Evidence in Stratigraphical Geology.

As regards the division of the entire series of stratified deposits into the above enumerated primary "systems," the value of palæontological evidence has never been disputed. In any given country, it would be possible, undoubtedly, to determine the order and relative succession of the great formations, to some extent at any rate, by a mere appeal to the mineral character and order of superposition of the rocks themselves; but it is perfectly clear that this method of procedure would necessarily break down totally the moment we came to try and determine which were the corresponding formations in some far-distant region. By the stratigraphical evidence alone we could determine the relative position and age, for example, of the Silurian, Devonian, and Carboniferous systems in Britain; but it would be an entire impossibility to identify these same systems, say in North America, except by means of the fossils which they contain. So far, then, as this goes, no question has ever been raised as to the value and powers of Palæontology; but when we come to consider the minor rock-groups included in these systems, we find much difference of opinion as to the extent to which the evidence of the fossils is available in determining stratigraphical horizons. Part of this difference of opinion is due to imperfect acquaintance on the part of stratigraphical geologists with the methods of palæontological inquiry, and needs no discussion here; but part is well founded, and either arises from actual defects in the modes of research employed by palæontologists, or is due to the fact that the conditions under which different systems, or different portions of the same system, have been deposited have not been identical, and that conclusions which might be well founded in one case might be found to break down in another apparently similar case. To both of these points a brief consideration may be given.

As regards imperfections in the methods of palæontological research, by far the most important arises from the fact that too much weight has been attached by observers, especially in the earlier periods of the science, to the *age* of the rocks in which any given fossil occurred. So long as the opinion was current that fossils occurring in different formations were necessarily different, it followed of necessity that the smallest and most trivial varietal, or even individual, peculiarities of form or structure were considered as sufficient to establish specific distinction. At present, however, palæontologists are tolerably agreed that the mere fact of a difference of physical position, and consequently of age, ought not to be taken into account in considering the true affinities and systematic position of a fossil. At the same time it is, for many reasons, most important that palæontologists should have a general personal acquaintance

with the rocks in which occur any fossils that they may have to examine and describe; and many errors have arisen from the neglect of this sound rule.

Again, it is now clearly recognised that in any comparison between two sets of beds by means of their fossils, with a view of ascertaining their relative age, it is essential to take into account *the conditions under which the deposits in question were formed.* Thus, two marine deposits, both accumulated in shallow water, can be fairly and fully compared with one another, but they can only be imperfectly compared with a deposit formed in a deep sea, and they cannot be compared at all with deposits which have been formed in inland fresh waters or on land. Hence we find that palæontologists have differed, and still differ, widely with regard to the relative value as tests of the age of strata, to be assigned to different *classes* of fossils. In certain cases—some of which will be more fully referred to subsequently—a different age would be assigned to a group of beds on the strength of its vegetable remains to that which would be deduced from a study of the animal fossils of the same or of associated beds. Or, the marine Invertebrate fossils in some cases may point to one age for the beds, while the remains of Vertebrates indicate another. Such cases must be dealt with on the following general principle :—

Deposits containing numerous land-plants or the bones of terrestrial Vertebrates are mostly estuarine, lacustrine, or fluviatile in origin, though in some cases they have been formed on land. On the other hand, deposits containing marine Invertebrates have been laid down in the sea itself, for the most part at moderate depths. There is, however, absolutely no reason for thinking that the succession of life as regards the land-plants and land-animals of any given region has been in any way parallel with the evolution of the marine animals of the seas of the same region. The evolution of the terrestrial organisms may have been much more rapid or much slower than that of the marine forms. Hence, it is quite possible that the land-plants and land-animals which are regarded as characteristic of a particular geological period, may be found coexisting with marine animals which are considered to characterise a different geological period. If, however, we take the stratified formations as a whole, we find that it is in the main by means of their marine faunæ that their relative age has been determined, the reason of this being the obvious one that the great majority of stratified deposits have been laid down in the sea, and the record of the succession of terrestrial organisms in time is a very incomplete one. The general chronological standard, as based upon palæontological evidence, is, therefore, founded mainly on the results afforded by the marine Invertebrates. In those cases, therefore, in which the marine deposits of a given series of beds would indicate through their Invertebrate fossils

a particular stage in chronological succession, while the fresh-water or terrestrial deposits of the same series through their vegetable remains would indicate another, it is to the former that we should give the precedence as determining the age of the entire series. Such cases are sometimes spoken of as instances of "homotaxis," but this is not strictly so. In the particular cases here in question, two sets of beds, which may have been formed contemporaneously, are found to contain fossils of apparently different geological ages, in consequence of the fact that the beds have been formed under different conditions, the one containing the remains of land-plants, and the other the remains of marine Invertebrates. The apparent difference of age is due to the fact that the evolution of the land-flora in the particular region where the beds are found has not been parallel with that of the marine fauna of the same region. On the other hand, "homotaxial" deposits, properly so called, are deposits which have been formed during the same geological period, and have been laid down under similar conditions, thus coming to contain similar classes of fossils, but which have been formed in regions very far apart. The similarity, or identity, of the fossils in the two sets of beds proves them to belong to the same general period; but their geographical remoteness is a proof that they were formed at different stages of this period, and that they were not precisely identical. Together with the similarity of certain types of life in "homotaxial" beds, there is found a dissimilarity as regards other types, this being a consequence of the fact that the two sets of beds have been formed in widely distant areas, and therefore in distinct zoological provinces. In other words, the dissimilarity in the fossils in "homotaxial" beds, in the strict sense of the term, is dependent on the *distance in space* of the beds, and is not due to difference of *origin*.

An excellent concrete example of the above general principle is afforded by the so-called "Dakota Beds" of North America. These are largely developed in the basin of the Upper Missouri, are mainly of brackish-water or fresh-water origin, and contain a series of plant-remains the general aspect of which is clearly Tertiary. If judged, therefore, by purely palæobotanical evidence, the "Dakota Beds" would be assigned to the Eocene system. The "Dakota Beds" are, however, overlain by some thousands of feet of stratigraphically younger deposits charged with marine fossils of Cretaceous type. Judged, therefore, by a palæozoological standard, the "Dakota Beds" must be assigned to the Cretaceous period. The explanation of this discrepancy in the age of the beds as deduced from the plants and animals respectively is apparently twofold. On the one hand, the "Dakota Beds" are mainly of fresh-water origin, whereas the strata by which they are surmounted were laid down in the sea. On the other hand, we must suppose that the Tertiary flora had been introduced into the American area at a time when the seas of the same area were still tenanted by the characteristic animals of the Cretaceous period, and that the latter were not replaced by the animals distinctive of the Tertiary period until long after the land-vegeta-

tion had assumed the Kainozoic facies. That the "Dakota Beds" are truly of Cretaceous age is further shown by the fact that part of the series is marine in origin, and that in it are met with the remains of such characteristic Cretaceous types of Invertebrates as Ammonites and Belemnites.

A somewhat more complicated case is that of the so-called "Laramie Beds," or "Lignitic Series," of North America. These constitute a series of beds, of some thousands of feet in thickness, which repose upon strata with marine fossils of unquestionable Cretaceous type, and are unconformably surmounted by strata containing equally unquestionable marine Tertiary (Eocene) fossils. The "Laramie Beds" are admittedly of purely inland origin, and were probably laid down in a vast brackish-water lake. The Invertebrate fossils which they contain consist almost wholly of brackish-water, fresh-water, and terrestrial Molluscs, and the characters of these are such that they do not afford a decisive test of the age of the series. The remaining fossils are mostly those of land-plants or of terrestrial Vertebrates, and the evidence as to age yielded by these respectively is discrepant, the vegetable remains being of distinctly Tertiary type, while the Vertebrates belong to the characteristic Mesozoic group of the Dinosaurian Reptiles. When we consider, however, that the evidence afforded by the "Dakota Beds" and the strata overlying these renders it certain that the Tertiary vegetation had been introduced into America at a time when the marine Invertebrates of the Cretaceous period still existed in full force, we cannot attach much value to the plant-remains of the "Laramie Group" as indicating a reference of these strata to the Tertiary period. Adding to this consideration the presence of such characteristic Cretaceous Vertebrates as the Dinosaurs, and the further fact that the Laramie beds are surmounted *unconformably* by beds of unequivocal Eocene age, it seems difficult to resist the conclusion that these disputed strata are either truly of Cretaceous age, or that they form a transitional group between the Cretaceous and the Tertiary systems.

A good example in the European area of the contradictory evidence sometimes yielded by different classes of fossils as tests of age is afforded by the "Pikermi Beds" of Attica. These beds contain an abundance of the remains of terrestrial Mammals, which have generally been regarded as of a distinctively Miocene type; and on the strength of this the "Pikermi Beds" have been referred to the Upper Miocene period. The mammaliferous clays of Pikermi repose, however, upon strata containing marine Molluscs of unquestionable Pliocene type. The explanation of this appears to be, that the terrestrial Mammals of the Miocene period had persisted unchanged in the south-east of Europe, while the Miocene Mollusca of the Mediterranean had been replaced by the later Pliocene forms. Since it is by the marine Invertebrates that the age of strata can be most uniformly and most reliably judged, we are thus bound to refer the "Pikermi Beds" to the Pliocene period.

Contemporaneity and Homotaxis.

The discovery of the use of fossils as tests of the age of the sedimentary rocks, and the recognition of the fact that by their means a chronological succession of the stratified deposits of any particular region could be established, constituted great advances in geological

science, as also in Palæontology itself, but they led at first to erroneous generalisations. When it had been clearly established that particular groups of strata in Europe were characterised by particular assemblages of animals and plants, it was, not unnaturally, concluded that similar or identical assemblages of organisms would be found to characterise corresponding groups of strata all over the world. This led to the idea that the successive faunæ and floræ observable in the area first examined had been *universally distributed over the whole globe;* from which followed the old catastrophistic view that the close of each geological period had been signalised by a more or less complete extinction of the animals and plants then in existence, and that a new fauna and flora had been introduced at the commencement of each succeeding period.

It is, however, now universally admitted that in nature the chronological succession of the rocks, as determined by fossil remains, is local and not universal—in the sense that the precise order of phenomena must necessarily have differed in different regions. That this must be so is proved by the existence at the present day of "zoological provinces"; by the fact that dry land and sea must always have existed since the beginning of Palæozoic time at any rate, and that sedimentation can, therefore, never have been universal; and by the certainty that the sedimentary deposits now in process of formation, and therefore necessarily coeval, contain the remains of dissimilar groups of animals and plants.

In view of these considerations, it is necessary to consider what precise significance is to be attached to the term "contemporaneous" as applied to different groups of strata. When groups of beds in different parts of the earth's surface, however widely separated from one another, contain the same fossils, or rather an assemblage of fossils in which many identical or closely allied species occur, they are generally said to be "contemporaneous"—that is to say, they are ordinarily supposed to belong to the same geological period, and to have been formed at the same time in the history of the earth. They would therefore be ordinarily regarded as "geological equivalents," and would be classed as Silurian, Devonian, Carboniferous, and so on. The use of the term "contemporaneous" in the above comprehensive sense cannot, however, be accepted without serious qualification. Within the limits of a single geographical area of moderate size, beds containing identical, or nearly identical, fossils, may doubtless be safely regarded as strictly "contemporaneous," since there is no reason why such should not have been deposited within one ocean, and during a single geological period. When, on the other hand, we find precisely identical or even representative species of fossils in beds which are very widely removed from one another geographically, there is a presumption that such beds are *not* exactly

contemporaneous, but that they succeeded each other in point of time, though not necessarily by any very long interval geologically speaking. The general ground for this presumption is the readily intelligible one that such beds, if sufficiently far apart, must have been deposited in different oceans, but that we cannot suppose that any given species could have been developed to begin with in more than one ocean. When, therefore, we find identical species in strata in two widely remote areas, we are forced to conclude that these species must have appeared sooner in one area than in the other, and that the one set of strata must be later than the other, if by no more than the time required for the migration of these species from their original area to the other.

Most of the facts bearing upon this question may be elicited by a consideration of such a well-known and widely extended group of deposits as the marine division of the Carboniferous system, of which the chief member is the Carboniferous Limestone. This group of deposits is more or less extensively developed in regions as remote from one another as Europe, Central Asia, China, Japan, Australia, South America, and North America; and it is characterised by an assemblage of distinctive fossils, among which certain species of Brachiopods are specially noteworthy. Not only are the Carboniferous Brachiopods in these widely distant areas referable to the same *genera* (*Producta*, *Athyris*, *Streptorhynchus*, &c.), but identical *species* are in some cases found to range over the greater part of the vast area occupied by these deposits.[1] Now, if we believe that the Lower Carboniferous rocks in all these widely distant regions were "contemporaneous," in the sense that they were deposited at precisely the same time, we should be compelled to admit the existence during Carboniferous time of an ocean embracing all these points, and, in spite of its enormous extent, so uniform in temperature, depth, and the other conditions of marine life, that organisms either the same, or very nearly the same, inhabited it from end to end. We can, however, point to no such uniformity of conditions and consequent uniformity of life over any such vast area at the present day; and we have, therefore, no right to assume that this is the true explanation of the facts. Moreover, all that we know of the geographical distribution of recent organisms would prove that these identical species cannot have been produced simultaneously in all the areas where their remains are now found, but that they must have been dispersed

[1] Among the commoner and more characteristic types of Brachiopods found in the Lower Carboniferous rocks of Europe, *Producta semireticulata*, *P. longispina*, *P. aculeata*, *P. costata*, and *Streptorhynchus crenistria* occur, along with other European forms, in the Carboniferous rocks of China (Kayser). All these species, with the exception of *P. costata*, have been identified in the Carboniferous deposits of Australia and India; and all of them occur, with various other European types, in the Lower Carboniferous rocks of North America.

from one or other of these areas, or from some point still unknown; and this dispersal must necessarily have consumed a long period of time. Any other view would lead us almost inevitably to the now abandoned theory that each period in geological history was characterised by a special group of organisms spreading over the whole globe, and that there took place at the close of each period a general destruction of all existing forms of life, and a fresh creation of the new forms characteristic of the next period.

In our inability, then, to accept this view, we must seek for some other explanation of the observed facts. The most probable view, and the one which is supported most strongly both by what we see at the present day and by what we learn from numerous examples in past time, is this: The Carboniferous Limestone—to take this member of the Lower Carboniferous deposits in particular — was not deposited all over the world in one given period, by one sea, or at exactly the same time; so that it cannot be said to be strictly "contemporaneous" wherever it is found. This would imply a uniformity of conditions over vast distances, such as exists nowhere at the present day, and such as we have no right to assume ever existed. On the contrary, the deposition of the Carboniferous Limestone must have first taken place in one comparatively limited area—say in Europe—where fitting conditions were present both for the animals which characterise it, and for the formation of beds of its peculiar mineral and physical characters. How wide this area may have been, signifies very little. It may have been as large as the area now covered by the Pacific, or larger, and yet it could not include all those localities in which strata of Lower Carboniferous age with identical or representative fossils are already known to exist. Under any circumstances, some dispersion of the species of the original Carboniferous area must have been going on by the ordinary processes of migration from the commencement of the Carboniferous period, but this dispersion must have been greatly accelerated towards the close of the period of the deposition of the Carboniferous Limestone. At this time the conditions present in the original area must be supposed to have become unsuitable for the further existence in that area of the assemblage of animals which had been its inhabitants, or, at any rate, for a great many of them. The change from suitable to unsuitable conditions must, it is hardly necessary to say, have been an extremely slow and gradual one, and would doubtless be connected with the progressive shallowing of the sea, the diversion of old currents of heated water, or the incoming of new currents of cold water, or other physical changes tending to alter the climatic conditions of the area. What, then, would be the effect of such a change of conditions as we have supposed, upon the animals inhabiting the area? —Some of them would, doubtless, be sufficiently hardy and accom-

modating to bear up under the new state of things; and these would persist into the ensuing period, without any perceptible change, it might be, or more probably in the form of varieties or species allied to the old ones. In this case, therefore, we should get a certain number of species which would pass from the Carboniferous Limestone up into the Yoredale series, the Millstone Grit, or the Coal-measures; or, if we did not find any species exactly the same in all these groups, we should still find in the later groups some forms which would be varieties of those of the older, or which would be allied or representative species.

There would, in the second place, be a certain number of species which would be utterly unable to withstand the altered conditions of the area; and these would gradually die out and become wholly extinct. We should thus get a certain number of fossils which would be either exclusively confined to the Carboniferous Limestone in general, or which, perhaps, might not be found out of the Carboniferous Limestone of a single region, or even of a single particular locality.

Lastly, some species would yield so far to the altered conditions of the area that they would "migrate," and seek elsewhere a more congenial home. This term is apt to convey false impressions; and it will be well here to consider what is meant by the "migration" of species or groups of animals. It is quite obvious that only animals like birds, mammals, insects, &c., which enjoy when grown up the power of active locomotion, can actually "migrate" in person, supposing they find themselves placed under unfavourable conditions. There are many animals, however, such as most Molluscs, Corals, Polyzoans, &c., which have, when adult, either no power of changing their place, or at best a very limited one. Still in these cases even, though the *individual* has no means of removing his quarters to some more favoured spot, there may be a "migration" of the *species* from an unsuitable to a suitable locality. This is effected through the medium of the young, which have the power of choosing where they will settle, and are endowed with vigorous powers of locomotion. If, for example, a bed of oysters should become placed under conditions unsuitable for the development of these Molluscs, it is clear that the old oysters cannot change their location. The young oysters, however, swim about freely; and these will move away from the original bed till they find a place which will suit them. By a repetition of this process there may be in course of time a removal or "migration" of a species to almost any distance, irrespective of the fact that the adult is permanently rooted.

To return, then, to the case which we have been considering: When the conditions of life in the seas of the Carboniferous Limestone became unfavourable for the further existence of their fauna,

some species would migrate to a more congenial area. In this way a greater or less number of the species characteristic of the Carboniferous Limestone would ultimately be transferred to some other area. Here they would mingle with the forms already inhabiting that area, perhaps more or less completely supplanting these, or perhaps merely succeeding in maintaining a more or less precarious existence. In either case, their remains would be preserved in the sedimentary deposits of the new area. When, ages afterwards, we come to examine the crust of the earth geologically, we should find these identical and characteristic species of fossils in the rocks of the two areas, and we should say—"these rocks are contemporaneous." It is clear, however, that we should be wrong in so saying. The rocks in question would belong to the same geological period, but they would belong to different stages of the same period, and they would not be strictly contemporaneous. For deposits of this nature, believed to hold this relation to each other, the term of "homotaxial" has been proposed, in place of the term "contemporaneous."

What has just been said about the Carboniferous rocks would apply with equal justice to all the great formations, and to many of the smaller rock-groups all over the world. The Ordovician and Silurian rocks of Europe, North America, South America, Australia, &c., contain very similar fossils, and are undoubtedly "homotaxial." Nothing, however, that we see at the present day can justify us in believing that these widely separated deposits are strictly "contemporaneous," in the sense that they were deposited at exactly the same period of time. We should have to believe, if this conclusion is to be justified, that in Ordovician and Silurian times the ocean spread over a much larger area of the earth's surface than it does now, and that its temperature and depth were unnaturally uniform; and there are, perhaps, some who would accept this view. What has been said about the Ordovician and Silurian rocks as a whole, applies with still greater force to certain of the minor subdivisions of the same, which contain many of the same specific forms in parts of the globe very widely removed from one another. It is the very identity of the fossils, however, which proves that the beds in question, from their geographical position, cannot have been deposited at exactly the same time, though they doubtless belong to the same period, and may even be said to be related to one another, so far as their identical fossils are concerned, by lineal descent. Similar remarks might be made about the Devonian, Permian, Triassic, Jurassic, Cretaceous, and other formations; but it is not necessary further to multiply examples.

If we consider the present state of things upon the globe, we shall be further convinced of the justice of these views, which were first prominently brought forward in Britain by Professor Huxley.

If we could suddenly remove the sea from the earth, we should find at various points of the earth's surface deposits of different kinds, now concealed from us by the ocean, or only partially known by dredgings or soundings. Thus we should find vast accumulations of calcareous matter, in the form of coral-rock and coral-reef, where now rolls the Pacific Ocean. In high northern and low southern latitudes we should find great deposits of sand and mud, with angular blocks of stone, the whole derived from the ice-clad regions of the poles. Over vast areas, again, in the deep Atlantic, we should find an impalpable chalky mud, or "ooze." All these different deposits are obviously and necessarily "contemporaneous," not only in the geological acceptation of the word, but in its most literal sense. In spite of this fact they would not contain the same fossils; and, indeed, they would be characterised by organic remains which would be wholly different in each case. The coral-reefs of the Pacific would be essentially characterised by the abundance of the remains of reef-building corals, though they would also present other tropical forms of life, especially Brachiopods and Echinoderms. The glacial mud of the Polar regions would contain the remains of Arctic Molluscs, along with such other animals as delight in severe cold. Lastly, the ooze of the deep Atlantic would contain innumerable *Foraminifera*, along with siliceous Sponges and Crinoids. We learn, therefore, from this, that contemporaneous deposits not only do not necessarily contain the same fossils, but that, if widely separated geographically, they may be characterised by wholly dissimilar assemblages of organisms.

It may happen, again, as pointed out by Sir Charles Lyell, that deposits belonging to different geographical and zoological provinces may, as regards space, be nearly approximated, and, as regards time, may be actually contemporaneous, and yet may not contain any fossils in common, or only a very few. If, for example, any sudden upheaval were to lay bare what is now the floor of the Red Sea, together with that of the Mediterranean, we should find the two areas to contain deposits actually synchronous as regards the time of their deposition, and very near to one another in point of distance, and yet containing, upon the whole, entirely distinct groups of organic remains. We learn, therefore, from this, that owing to the existence of geographical barriers, it is possible for contemporaneous deposits to be found in close contiguity, in a single region, and yet to contain very different fossils.

Again, it has been abundantly proved that even within the limits of a single ocean deposits are now in process of formation which, though strictly contemporaneous in point of time, nevertheless differ from one another altogether both in mineral characters and in their included organic remains. Thus, the mechanical deposits formed

on the borders of an ocean, in the neighbourhood of land, differ wholly in mineral character from the peculiar "muds" formed in the profound depths of the same ocean; an equal difference existing as to the character of the animals buried in each. We thus learn that marine deposits may be strictly contemporaneous, and may be placed near to one another in point of distance, and yet may be wholly unlike both lithologically and zoologically. Lastly, synchronous deposits necessarily contain wholly different fossils, if one has been deposited by fresh water and the other has been laid down in the sea. The fresh-water deposits of one period are obviously contemporaneous with the marine formations of the same period, and they may not be far removed from one another in point of distance, but they must contain altogether different organic remains. The former will contain remains of the fresh-water and terrestrial animals of the period, and of these only; whilst the latter will principally, if not exclusively, be characterised by the remains of marine forms of life. In this way, there is reason to believe, may be explained the differences between the fossils of the Old Red Sandstone and of the Devonian rocks, strictly so called. Both are believed to have been deposited in the same geological period, and to be truly "contemporaneous"; but they do not contain the same fossils. This may be readily explained, however, if we suppose the former to represent the fresh-water deposits of the Devonian period, or to have been laid down in an inland sea, whilst the latter is the true marine formation of the same period.

In the strictest sense, then, of the term, deposits may be spoken of as "homotaxial" when they contain identical or closely allied fossils, but have nevertheless not been laid down at precisely the same time. If such deposits are widely separated from one another in space, then the possession of identical fossils is a direct argument in favour of a want of absolute contemporaneity—supposing that the deposits compared have been formed under similar conditions, in which case alone a complete comparison is possible. Thus, the Lower Carboniferous rocks of Britain, Russia, China, and North America are all marine in origin; and the fact that they contain identical species of Brachiopods is thus an argument in favour of the view that they were not formed at *precisely* the same time, since they are so widely apart that they cannot be regarded as having been simultaneously laid down within the limits of a single ocean. Nevertheless, the deposits in question were laid down in the same geological period, and are therefore "geological equivalents." The doctrine of "homotaxis," therefore, if rightly limited and defined, in no way diminishes the value of fossils as indicative of the age of the formations in which they occur. If we give the term "contemporaneous" a purely geological sense, and

endeavour to forget its literal signification as applying to events which have occurred at precisely the same moment of time, then it is just as good an epithet for the different deposits belonging to a given geological formation as is the term "homotaxial." All the deposits which possess Carboniferous fossils, at whatever point of the earth's surface they may be situated, belong to the Carboniferous period, and are therefore geologically contemporaneous. All that is really implied by the doctrine of "homotaxis," rightly regarded, is that we cannot say that any great formation in any one country is the precise equivalent of the same formation in any country very widely removed in point of distance, in the sense that its deposition began and ended at exactly the same times; and therefore we cannot parallel the subdivisions of such formations with anything approaching to absolute precision. Regarded as a whole, however, the Carboniferous formation of America is the geological equivalent of the Carboniferous formation of Europe, and both belong to what geologists understand as the "Carboniferous period." As the same is true of all the great formations, in all parts of the world, it is clear that the principal advantage of the use of such a term as "homotaxis" is simply that we thereby avoid the employment of a word which common usage would wrongly interpret; and it is quite certain that we cannot abolish the idea of *geological* "contemporaneity," as demonstrated by the presence of identical or representative species of fossils; nor can we refuse to admit that formations containing such fossils, however far removed from one another in point of distance, must have been laid down within the limits of the same great "period" in the history of our earth.

In the case of the Lower Carboniferous deposits above alluded to, not only are the fossils generally similar to one another in all the widely separated regions in which these strata have been recognised, but certain characteristic *species* seem to have an almost universal distribution. The enormous range of certain specific types remains a most noteworthy fact, whatever explanation may be given of it. As a general rule, however, deposits in different geographical areas, which occupy a corresponding position in the series of the stratified rocks, and are therefore geologically speaking "contemporaneous," contain but few or no actually identical *species*. The faunæ of such deposits, on the contrary, are usually composed of allied or representative forms, the same groups of animals being the ones prevalent in and characteristic of the deposits, but the *species* being different. Thus, there can be no doubt that the Devonian deposits of North America and Western Europe are geological equivalents, since they occupy in each region the interval between the highest Silurian and the lowest Carboniferous sediments. The fauna of the Devonian rocks of North America, also, presents a close general resemblance to that of the Devonian of Devonshire, Belgium, and Germany. In both cases there is a predominance of certain special groups of animals, amongst which the great Hydrozoal group of the Stromatoporoids may be particularly singled out. The Stromatoporoids of the American

Devonian represent those of the European Devonian, and certain peculiar generic types (such as *Idiostroma*) are common to both regions ; but there is, nevertheless, a marked difference as regards the forms most prevalent in each. Thus, the European Devonian is specially characterised by the prevalence of species of *Actinostroma* and *Stromatopora*, while the most characteristic types of the American Devonian belong to the genus *Clathrodictyon*, a genus which in Europe attains its maximum in the Silurian period. Again, only few *species* of Stromatoporoids are common to the two regions in question. Precisely similar facts could be brought forward with regard to the Corals, Brachiopods, &c., of the Devonian formation in these areas ; and the general law which these facts illustrate would seem to be one of very wide application.

In other cases, while the general fauna of two geologically equivalent deposits in widely remote areas is broadly similar, special organic types may occur in one or other area which indicate a later or an earlier age than that pointed to by the general assemblage of fossils. A marked example of this is found in the occurrence of such characteristic Secondary types of Cephalopods as *Ammonites* and *Ceratites* in certain strata in North-western India, the general fossils of which are of unequivocal Carboniferous type (Waagen). In this case, special organic types which are in general characteristic of a later age, are associated with a general fauna distinctive of an earlier period. An instance of the opposite of this —*i.e.*, of the occurrence of a special organic form of an earlier period in association with a general fauna of a later type—is found in the occurrence of Ammonites in California in strata containing abundant fossils characteristic of the Eocene Tertiary.

Geological Continuity.

We are now in a position very briefly to discuss the question of what may be called "geological continuity." It has already been stated that the entire series of Fossiliferous or Sedimentary rocks may be naturally divided into a certain number of definite rock-groups or "formations," each of which is characterised by the possession of a peculiar and characteristic assemblage of fossils, constituting, or rather representing, the "life" of the "period" in which the formation was deposited. The older geologists held, what probably every one would be tempted to think at first, that the close of each formation was characterised by a general destruction of the forms of life of the period, and that the commencement of each new formation was accompanied by the creation of a number of new animals and plants, destined to figure as the characteristic fossils of the same. This theory, however, not only invokes forces and processes which it can in no way account for, but overlooks the fact that most of the great formations are separated by lapses of time, unrepresented perhaps by any deposition of rock, or represented only in some particular area, and yet, perhaps, as great as, or greater than, the whole time occupied in the production of the formation itself.

Upon any theory of evolution, however, it must be held that

there was no such sudden destruction of life at the close of each great geological epoch, and no such creation of fresh forms at the commencement of the next period. On the contrary, it is certain that there is a geological "continuity," such as we see in other departments of nature, and that the lines which we draw between the great formations merely mark periods of time in which no rocks were laid down, or the rocks deposited in which are at present unknown to us.

What are we to believe occurred at the close of any great geological period—say, the Cretaceous period? If we reject the view that the close of the period was marked by a sudden and universal extinction and destruction of the characteristic Cretaceous forms of life, there is only one other view which we can take. Confining our attention solely to those seas of the period of which alone we know enough for safe reasoning, we know that the close of the Cretaceous period in Europe was accompanied, or rather caused, by an upheaval of the Cretaceous area, and an obliteration of the Cretaceous sea. This upheaval was, of course, effected with extreme slowness, or, at any rate, not suddenly, and it must have completely changed the life-conditions or "environment" of the animals which swarmed in the Cretaceous seas. Some of these would doubtless be unable to accommodate themselves to their altered surroundings, and would simply die out. Others, we may presume, would migrate to some more favourable area, and some of these might accomplish their migration without undergoing any change. Most of the forms which migrated, in the process of migration, and by reason of coming into contact with strange neighbours and untried conditions, would, however, probably undergo more or less modification. Ultimately, therefore, many characteristic Cretaceous forms might be transferred to some sea far distant from their original home. Not only so, but some of the transferred species might have suffered so much modification that they would no longer be regarded as specifically identical with the original Cretaceous forms, but would be looked upon simply as allied or "representative" species, though really the lineal descendants of the animals of the Chalk.

It is perfectly clear that the process of rock-deposition which was going on in Europe towards the close of the Cretaceous period was not, and could not be, abolished by the elevation of the European area, and the obliteration of the Cretaceous sea, but was simply *transferred* to some other area. In this particular case, we do not happen to know where the new area of deposition may have been. It is quite certain, however, that in whatever area the Cretaceous animals took refuge, there rocks must have been deposited in course of time, as they are in all seas, though it does not in the least follow that the rocks of this new era should have the smallest likeness in

mineral composition to the Cretaceous sediments. If we should at any time discover these rocks, it may pretty safely be predicted what we should find in them in the way of fossils. We should find, namely, some Cretaceous species, probably unchanged; with these there would be forms allied to the Cretaceous species, but differing from them to a greater or less extent; in addition, there would be a certain proportion of forms of life wholly unknown in the Cretaceous rocks; and lastly, there would be a conspicuous absence of certain characteristic species of the Chalk period. In other words, such deposits as we have been speaking of would contain an assemblage of fossils more or less intermediate in character between those of the true Cretaceous period and those of the lowest Tertiary beds (Eocene), which rest upon the Chalk; or they would present an intermixture of Cretaceous with Eocene types. In point of fact, we have fragments of such intermediate deposits (in the Maestricht beds of Holland, the Pisolitic Limestone of France, the Faxoe Limestone of Denmark, and the Thanet Sands of Britain), and we find in them traces of such an intermixture. Moreover, when we come to examine the boundary-line between the Cretaceous and Tertiary in other regions, we do actually meet with strata which have been deposited during the period marking in Europe the interval between the White Chalk and the lowest Tertiary deposits, and which contain, therefore, an intermixture of Cretaceous and Eocene types of life. The most celebrated of these transitional formations, so far as known, is the "Laramie Group" of North America, the precise position of which in relation to the strata above and below has been a matter of much controversy.

We may pause here to consider how it is that we may never hope to find a complete series of deposits linking on one great formation to another, as, for example, the Chalk to the Eocene rocks. In the first place, only a limited portion of the earth has as yet been properly examined, and we have therefore no right to expect that we have as yet hit upon the area, or areas, to which the process of rock-forming was transferred at the close of the Cretaceous period proper in Europe. We have, however, the full right to expect that we shall ultimately find formations which will have to be intercalated in point of time between the White Chalk and the Eocene; and, as before said, examples of such are already known to us. In the second place, we have every reason to suppose that many of these intermediate deposits have been destroyed at some period subsequent to their formation by what is technically called "denudation," or, in other words, by the action of rain, rivers, ice, and the sea. In the third place, many of the missing deposits may have been concealed since their formation by the deposition upon them of other newer rocks; or they may be situated in areas which are at

present covered by the ocean. Lastly, we must not forget that there may have been times in which great changes in life were actively progressing in areas in which there might be little or no contemporaneous deposition of rock, so that the extreme terms of a series might be preserved to us whilst all the intermediate links might have escaped record.

From these and similar causes, it is certain that we shall rarely be able to point to a complete series of deposits linking one great geological period, such as the Cretaceous, to another, such as the Eocene. Still, we may well have a strong conviction that such deposits must exist, or must have existed, as memorials of, at any rate, part of the time which elapsed between the close of the one formation and the commencement of the next. Upon any theory of "evolution," at any rate, it is certain that there can be no total break in the great series of the stratified deposits, but that there must have been a complete continuity of life, and a more or less complete continuity of deposition, from the Cambrian period to the present day. There was, and could have been no such continuity in any one given area; but the chain could never have been snapped at one point and taken up at a wholly different one. It remains certain, however, that we can never dispense with the division of the stratified series into definite rock-groups and life-periods. We can never hope to discover all the lost links of the geological chain, and the great geological systems will always be separated from one another by more or less evident physical or palæontological breaks, or by both combined. The utmost we can at present do is to arrive at the conviction that the lines of demarcation between the great formations only mark gaps in our knowledge, and that there can in nature be no *hiatus* in the long series of fossiliferous deposits.

Life-Zones.

While each geological rock-system is characterised by a general assemblage of distinctive types of animals and plants, the minor subdivisions of each system are likewise distinguished by the prevalence of particular forms of life. There are, no doubt, cases in which an extensive series of successive strata may appear to be characterised throughout by essentially the same organic types, there being apparently no restriction of special fossils to special horizons in the series. In so far as such cases have any real existence, they may be explained as instances in which a great series of sediments has been accumulated with such rapidity that there has been no time for marked biological changes, resulting in the dying out of old species and the introduction of new forms. In many cases, however, the apparent diffusion of the same kinds of fossils from the base to the summit of

a series of beds perhaps two or three thousand feet in thickness, is due simply to the fact that the organic remains met with in the formation have not been sufficiently investigated, and that the exact horizon at which each occurs in the series has not been accurately determined. The determination of the horizons of particular life-forms is a work of time, and demands both great stratigraphical knowledge and also a wide and accurate acquaintance with the characters of the fossils themselves—two requirements rarely fulfilled in the same individual.

In a considerable number of cases, however, it has now been shown that the fossils of a given formation may be divided into two principal groups. In the one group is comprised a series of common forms of life which may be regarded as characterising the formation *as a whole*. In the other group are included certain special fossils confined to particular parts of the formation, and characteristic of certain definite *horizons* or *zones* within the limits of the formation. All the great formations are to some extent capable of being broken up into minor rock-groups, characterised by special life-forms. Some of the differences in the kinds of fossils found in different parts of the same formation must, of course, be simply set down to the fact that different kinds of sediment imply changed conditions in the sea, and hence changes in the marine fauna. If, for example, part of a formation consisted of limestone and part of sandstone, we should expect, beforehand, to find that each of these rock-groups would have some fossils not found in the other, since the two would have been formed under different conditions. Apart, however, from differences arising from causes of this nature, we meet with cases in which a formation, even if essentially homogeneous in its mineral nature, can be divided into *zones*, each of which is characterised by the possession of special groups of fossils. Organisms belonging to any class of animals may serve in this way as test-forms (" Leit-fossilien ") for special horizons in a series of stratified formations, but there are particular groups of fossils which have been found to be pre-eminently available for this purpose. Among the older rocks of the earth's crust, the forms which have proved specially valuable for the determination of particular " zones " are the Graptolites, the Trilobites, and the Brachiopods, while the Cephalopods have been found to afford the most satisfactory tests in the case of the Secondary rocks. A well-known instance of this subdivision of a system of strata by means of special types of fossils is that afforded by the Ordovician and Silurian rocks of Europe, in which palæontologists, following Professor Lapworth, have recognised numerous well-marked " life-zones," characterised for the most part by the possession of particular types of Graptolites, though in some cases the distinctive fossils belong to other groups. Another well-

known example of the same phenomenon is afforded by the Jurassic deposits. These have been shown to contain a number of well-marked zones, each of which is characterised by the possession of some special fossils, and particularly by some special Ammonite. These zones are extremely constant, in any particular region, and they enable the observer to effect a division of the formation into special horizons, which have no stratigraphical existence, and are not separated by any physical break, but are of the utmost palæontological importance, and can be rendered readily available in working out the stratigraphy of any given area.

Certain life-zones appear to have nothing more than a local development and importance, but in other cases they have proved to be astonishingly constant even over very large areas. Perhaps the most remarkable known instance of the extension of particular life-forms over a vast area is that afforded by the Arenig rocks (a subdivision of the Ordovician system), which have been recognised as occurring in Europe, in Canada, and in Australia, and contain in all these widely remote areas the same peculiar types of Graptolites.

The principal difficulty that we have to confront in dealing with these "zones," is to produce any plausible explanation accounting for the destruction of the special life-forms of the one zone and the appearance of those of the next zone. For the most part, these zones are of very limited vertical extent, and they succeed each other in such a manner as totally to preclude the idea that the dying out of the old forms can have been in any way caused by a physical disturbance of the area. Perhaps the most probable view to adopt in the meanwhile is, that the formations in which distinct and limited life-zones can be recognised were deposited with extreme slowness; whereas those which show an essentially compact and homogeneous fauna from base to summit were deposited with comparative rapidity. Upon this view, a formation like the Lias is one formed by a process of very slow and intermittent sedimentation, the life-zones being separated by intervals, during which sedimentation must have been at a stand-still, but which were long enough to allow of more or less considerable biological changes, some forms dying out, or becoming modified, while other new ones came in. Upon this view, further, a formation like the Lias, though of comparatively small vertical extent, may represent as long a period of time as the whole of such a great formation as the Lower Carboniferous, which appears to have been formed under conditions of comparatively rapid sedimentation.

"Colonies."

It only remains in this connection to consider very briefly the doctrine of "colonies," laid down by M. Barrande, the eminent

Bohemian palæontologist. It has been laid down as a law that when once a species disappears it never again makes its appearance in the geological record. This is almost certainly true, so long as we remember that it can only apply to cases in which a species has entirely and totally disappeared from the earth, and that it is often very difficult, or altogether impossible, to obtain evidence as to the exact time at which a given species has thus become actually extinct. There are plenty of cases in which a species seemingly disappears in a particular set of rocks, to reappear in some higher and later set of rocks in the same region, whilst its remains are wanting in all the intermediate deposits of the area. It also often occurs that a species, having disappeared in one region, is found in deposits of a later age in another area. The above-mentioned law, therefore, can obviously only hold good of cases in which a species has definitely and finally become extinct; and this implies an amount of knowledge on our part which we seldom or never possess. M. Barrande, however, has endeavoured to prove that there are other cases in which groups of species peculiar to one set of beds may appear in a temporary and sporadic manner in a much earlier set of beds, the two deposits thus characterised being separated by beds containing fossils peculiar to the earlier and older series. Thus, the Ordovician and Silurian rocks of Bohemia are characterised by very distinct assemblages of fossils. According to M. Barrande, however, the Ordovician rocks contain in places a group of fossils characteristic of the Silurian series. The beds containing this "colony" of Silurian forms are succeeded by strata filled with Ordovician fossils; and it is only after several alternations of this kind that the Silurian fauna comes in definitely and generally. These temporary appearances of a later fauna in the midst of an older fauna are termed by M. Barrande "colonies," and he explains their occurrence as follows: If we suppose the seas of the Bohemian area to have been peopled with Ordovician animals at a time when other portions of Europe were covered by a sea containing Silurian animals, and suppose the former area to have been shut off from the latter by a land-barrier, we can readily understand how "colonies" might be produced. If, from any cause, a channel of communication were opened between the Bohemian area and the general area of Northern Europe, an immigration of species would take place from the latter into the former area. The Silurian species of the latter area would thus be imported, in greater or less numbers, into the midst of the general Ordovician fauna of Bohemia, and would be preserved in the Ordovician rocks. If, however, the channel of communication were speedily closed, so that the newcomers could not be constantly reinforced by fresh immigrants, the "colonial" species would die out, and the general Ordovician fauna would again reign supreme. A reopening of the channel of com-

munication would allow of a fresh immigration and the formation of a fresh "colony," and the process might be indefinitely repeated. Finally, however, we must suppose that the Bohemian area was permanently thrown open to immigration from the general European area, when the Silurian fauna of the latter would succeed in permanently and completely displacing the old Ordovician fauna of the former region. The phenomenon, therefore, of "colonies" may be defined as "the coexistence of two general faunas, which, considered in their entirety, are nevertheless distinct;" and it is to be regarded as merely a case of migration under certain peculiar and exceptional circumstances.

Not only have the phenomena described by M. Barrande in connection with his "colonies" never been recognised with any certainty in any region outside Bohemia; but there are strong grounds for believing that the actual facts in this area will not bear the interpretation which has been placed upon them by this distinguished palæontologist. Thus, Mr J. E. Marr, after a careful examination of the facts on the spot, was led to the conclusion that the so-called "colonies" have no real existence, but are the result of disturbances of the strata, being due, in reality, to the repeated "faulting down" of a band of the Silurian rocks among the underlying Ordovician deposits. This explanation seems to account adequately for the observed phenomena, and relieves us of the necessity of accepting a theory which can with difficulty be reconciled with the ascertained laws of the distribution of animals in past time.

CHAPTER IV.

THE IMPERFECTION OF THE PALÆONTOLOGICAL RECORD.

As has been already pointed out, the series of the stratified formations is an imperfect one, and is likely ever to remain so. The causes of this "imperfection of the geological record," as it has been termed by Darwin, are various; but it is chiefly to be ascribed to our as yet incomplete knowledge of the geology of vast areas of the earth's surface, to denudation, and to the fact that many of the missing groups are buried beneath other deposits, whilst more than half of the superficies of the globe is hidden from us by the waters of the sea. The imperfection of the geological record necessarily implies an equal imperfection of the "palæontological record"; but, in truth, the record of life is far more imperfect than the mere physical series of deposits. As we are here chiefly concerned with the biological aspect of the question, we may advantageously consider some of the main causes of the numerous breaks and gaps in the palæontological record at some length.

I. Causes of the Absence of Certain Animals in Fossiliferous Deposits.—In the first place, even if the series of the stratified deposits had been preserved to us in its entirety, and we could point to the sedimentary accumulations belonging to every period of the earth's history, there would still be enormous deficiencies in the palæontological record, owing to the differences in the facility with which different animals may be preserved as fossils. This subject is sufficiently important to render it advisable to consider each of the primary groups of the animal kingdom separately from this point of view:—

a. Protozoa.—As regards the sub-kingdom of the *Protozoa*, the Gregarines are destitute of hard parts, and have therefore left no traces of their past existence. The great majority of the Infusorian Animalcules are similarly destitute of hard parts, and are also unrepresented as fossils; though a few forms (*e.g.*, *Peridinium*) possess

an integumentary covering which under favourable circumstances is capable of preservation, and remains of these are believed to occur in some of the later sediments. Of the Rhizopods, the *Monera* and the most of the *Amœbea* have no hard structures, and are unknown as fossils, but a few of the latter possess a "test" which might possibly be preserved in the fossil condition. On the other hand, skeletal structures of lime or flint are almost always developed in the great Rhizopodous orders of the *Foraminifera* and *Radiolaria;* and these groups, therefore, have left abundant traces of their existence in past time.

b. Porifera.—A few of the Sponges (*Myxospongiæ*) are completely destitute of hard parts, and have therefore no palæontological history. The greater number of the *Porifera*, however, possess a calcareous or siliceous skeleton, which is more or less capable of fossilisation, and the record of such types is therefore a long and comparatively full one.

c. Cœlenterata.—Amongst the Cœlenterate animals, the Fresh-water Polypes (*Hydra*), the Oceanic Hydrozoa, the Jelly-fishes (*Medusidæ*), the Sea-blubbers (*Lucernarida*), the Sea-anemones (*Actinidæ*), and the *Ctenophora* are destitute of hard parts which could be preserved as fossils. The Jelly-fishes and Sea-blubbers, however, supply us with an instance of how a completely soft-bodied creature may leave traces of its past existence; for impressions left by the stranded carcasses of these animals have been detected in certain fine-grained rocks (*e.g.*, the Lithographic Slates of Solenhofen). On the other hand, the coralligenous Zoophytes or "Corals" (comprising the *Madreporaria* and most of the *Alcyonaria*) possess hard parts capable of preservation, and there are therefore few classes of organisms which are more fully represented in past time than the true Corals. As regards the *Hydrozoa*, most of the Hydroid Zoophytes have a horny skeleton, and do not become readily fossilised, though the large extinct group of the *Graptolites* is generally regarded as allied to the recent Sertularians. In a few of the *Hydractinidæ*, and in the whole group of the Hydrocorallines, a calcareous skeleton is present, and various fossil forms of these are known. In the great extinct group of the *Stromatoporoids*, now usually referred to the *Hydrozoa*, the skeleton was also of a calcareous nature.

d. Echinodermata.—Since the integument of the Echinoderms is liable to undergo more or less extensive calcification, this great division of animals is represented more or less completely in past time by all its sections. In the group, however, of the Sea-cucumbers (*Holothuroidea*), the calcareous structures so characteristic of other Echinoderms are reduced to their minimum; and accordingly, the evidence of the past existence of these animals is of a very limited description.

e. Annulosa.—The lowest division of the *Annulosa* (viz., that of the *Scolecida*) comprises animals almost without exception destitute of hard parts, and mostly living parasitically in the interior of other animals. With the exception, therefore, of some excessively problematical fossils which have been supposed to indicate the past existence of Ribbon-worms (*Nemerteans*), the palæontological history of the *Scolecida* is a total blank. Most of the true Worms (*Anarthropoda*) possess few or no structures by which we could expect to get direct evidence of their past existence. The Polychætous Annelides have, however, left ample traces of their former presence either by their horny jaws or by means of their investing tubes. There are also numerous fossils of the nature of burrows or "tracks" upon the mud or sand of ancient sea-bottoms, which have been regarded, with more or less probability, as having been produced by Annelides.

In the case of the higher *Annulosa* (*Arthropoda*), another law steps in to regulate their comparative abundance as fossils. Most, in fact almost all, fossiliferous formations have been deposited in water; and of necessity, therefore, most fossils are the remains of animals whose habits are naturally aquatic. As most deposits, further, are not only aqueous, but are also marine, most fossils are those of sea-animals. It follows, therefore, that the remains of air-breathing animals, whether these be terrestrial or aerial, can only be preserved in an accidental manner, so to speak—except the animal inhabit water (as the Cetaceans do), or except in the rare instances in which old land-surfaces have been buried up by sediment, and thus partially kept for our inspection. In accordance with this law, the most important and abundant fossil Annulose animals are *Crustaceans;* since these not only have a resisting shell or "exoskeleton," but are also generally aquatic in their habits. The air-breathing classes of the *Myriopoda* (Centipedes and Millepedes), the *Arachnida* (Spiders and Scorpions), and the *Insecta* or true Insects, on the other hand, have been much less commonly and completely preserved, though many of them are perfectly capable of being fossilised. Almost all such remains, moreover, as we have of these three great classes, are the remains of isolated individuals, which may have been accidentally drowned; or else they occur in hollow trees, or in fragments of ancient soils, or in vegetable accumulations such as coal and peat. There is, however, a considerable number of aquatic insects (but almost exclusively in fresh water), and there are many insects the larvæ of which inhabit water, whether this be fresh or salt; so that instances of these occurring as fossils are not very infrequent.

f. Molluscoidea.—With regard to the Molluscoids, the great majority of the *Polyzoa* and all of the *Brachiopoda* possess skeletal structures of a horny or calcareous nature, which are capable of preservation in the fossil condition. Both these classes of animals, therefore, possess

a long and tolerably complete palæontological record. In the case of the *Polyzoa*, however, the group of the fresh-water forms is not at present known to have any fossil representatives.

g. Mollusca.—This sub-kingdom requires little notice, since the greater number of its members possess hard structures readily capable of preservation in the fossil condition. Hence, all the great existing groups of Molluscs are more or less extensively represented in past time. The oceanic Pteropods, however, perhaps owing to their pelagic habit of life, or possibly as the result of their having fragile and easily destructible shells, have left a more incomplete record of their past existence than is the case with the other classes of Molluscs. Amongst the *Gastropoda*, again, the Sea-slugs and their allies (*Nudibranchiata*) possess no shell, and are unknown to the palæontologist; whilst the shell of the Land-slugs is extremely minute, and has only rarely been recognised as fossil. Lastly, the air-breathing terrestrial Molluscs, from their habits, rarely occur as fossils; whilst those which inhabit rivers, ponds, and lakes are less largely represented than marine forms, owing to the prepon derance of salt-water deposits over those of fresh water.

h. Tunicata.—The Tunicates, so far as living forms are concerned, are almost always destitute of skeletal structures, or possess only microscopic spicules of carbonate of lime. Only the most limited traces of the past existence of these animals have as yet been certainly detected; but it is quite probable that further investigations will considerably extend our knowledge on this point.

i. Vertebrata.—The majority of Vertebrate animals possess a bony skeleton, so that their preservation in a fossil state—so far as this point is concerned—is attended with no difficulty. Some of the fishes, however (such as the Lancelet, the Hag-fishes, and the Lampreys), have no scales, and either possess no "endoskeleton" or have one which is wholly or almost wholly unossified. The only evidence, therefore, which could be obtained of the past existence of such fishes would be afforded by their teeth; but these are wanting in the Lancelet, and are small and horny in the Lampreys: so that we need not wonder that these fishes are unknown as fossils. The higher groups of the fishes, however, taking everything into consideration, may be said to be abundantly represented in a fossil condition by their scales, bones, teeth, and defensive spines.

The Amphibians are tolerably well represented by their bones and teeth, and, as regards one extinct order, by integumentary plates as well. They have also left many traces of their existence in the form of footprints. Most living Amphibians, however, frequent fresh waters, or spend a great part of their time upon the land; and hence their remains would not be likely to be preserved in marine deposits.

The abundance of Reptiles as fossils naturally varies much, according to the habits of the different orders. Of the living orders, the Chelonians (Tortoises and Turtles) are by no means rare; since many of them are habitual denizens of fresh water or of the sea, whilst all are provided with a well-developed skeleton. The existing *Squamata* (Lizards and Snakes) and the *Rhynchocephalia* live chiefly upon the land, and do not therefore abound as fossils; but some extinct types of the former (the Mosasauroids) were marine in their habits, and have consequently been pretty fully preserved. The *Crocodilia*, again, are so essentially aquatic in their habits, that their comparative frequency in aqueous deposits is no matter of wonder, especially if we recollect that many of the extinct members of this order frequented the sea itself. Of the extinct orders of Reptiles, the great *Ichthyosaurs* and the *Plesiosaurs* and their allies were marine in their habits, and their remains occur in what may fairly be called profusion. The Flying Reptiles, or *Pterodactyles*, would not seem to have any better chance of being preserved than Birds, if as good, yet their remains occur by no means very rarely in certain formations. The terrestrial *Dinosaurs* and *Anomodonts*, again, come very much under the laws which regulate the preservation of Mammals as fossils; and their remains are chiefly, but not exclusively, to be found in fluviatile or estuarine deposits.

As regards Birds, their powers of flight, as pointed out by Sir Charles Lyell, would save them from many destructive agencies, and the lightness of their bones would favour the long floating of the body in water, and thus increase the chances of its being devoured by predaceous animals. In accordance with these considerations, the most abundant remains of Birds belong to species which frequent the sea-shore, lakes, estuaries, or rivers, or which delight in marshy situations; though in certain regions the principal fossil representatives of the class *Aves* are large wingless forms, of terrestrial habit, and with their bones largely filled with marrow instead of air.

Lastly, as regards Mammals, the record is far from being a full one, and from obvious causes. The great majority of Mammals live on land, and therefore are not likely to be buried in aqueous, and especially in marine, accumulations. That this cause is the chief one which has operated against the frequent preservation of Mammalian remains is shown by the fact that when we exhume an old land-surface, the remains of Mammals may be found in tolerable plenty. The strictly aquatic Mammals—such as Whales, Dolphins, and the like—are, of course, much more likely to have been preserved as fossils than the strictly terrestrial forms; but their want of integumentary hard structures places them at a disadvantage in this respect as compared with fishes. In a general way, we may conclude that the preservation of the terrestrial Mammals as fossils is due to

the occurrence of individuals being killed whilst swimming a river or some other piece of water, or being mired in a bog, or to the bones of those that had died on land being washed into some stream, and thence into a lake or into the sea, by floods; but there are other cases for which a different explanation must be sought. The most abundant remains of Mammals have been found in deposits which have been laid down in lakes.

II. Unrepresented Time.—In the second place, we have seen that the *geological* record is very imperfect, and this of necessity causes vast gaps in our palæontological knowledge. In this connection we may briefly consider the evidence which we possess as to the immensity of the "unrepresented time" between some of the great formations, and no better example can be chosen than that of the Cretaceous and Eocene rocks, as developed in Europe. In considering such a case, the evidence may be divided into two heads, the one palæontological, the other purely physical, and each may be looked at separately.

The Chalk, as is well known, constitutes in Britain the topmost member of the Cretaceous formation, and is the highest deposit there known as appertaining to the great Secondary or Mesozoic series. It is directly overlaid in various places by strata of Eocene age, which form the base of the great Tertiary or Kainozoic series of rocks. The question, then, before us is this, What evidence have we as to the lapse of time represented in Britain merely by the dividing-line between the highest beds of the Chalk and the lowest beds of the Eocene?

Taking the palæontological evidence first, it is found that not a single specific type out of the vast number of known Cretaceous fossils has hitherto been recognised with certainty as occurring in the immediately overlying Eocene beds. These latter, on the contrary, are replete with organic remains wholly distinct from those of the Cretaceous beds. It may be said, therefore, that the very extensive assemblage of animals which lived in the later Cretaceous seas of Britain had entirely passed away and become a thing of the past, before a single grain of the Eocene rocks had been deposited. Now it is of course open to us to believe that the animals of the Chalk sea were suddenly extinguished by some natural agencies unknown to us, and that the animals of the Eocene sea had been in as sudden and as obscure a manner introduced *en masse* into the same waters. This theory, however, calls upon the stage forces of which we know nothing, and is contradicted by the whole tenor of the operations which we see going on around us at the present day. It is preferable, therefore, to believe that no such violent processes of destruction and repeopling took place, but that the marked break in the life of the two periods indicates an enor-

mous lapse of time. The Cretaceous animals, in consequence of the elevation of the British area at the close of the Cretaceous period, must have mostly migrated, some doubtless perishing, and others probably becoming modified in the process. When the British area became once more submerged beneath the sea, and became again a fitting home for marine life, an immigration into it would set in from neighbouring seas. By this time, however, the Cretaceous animals must have mostly died out, or must have become greatly changed in their characters; and the new immigrants would be forms characteristic of the Lower Eocene. How long the processes here described may have taken, it is utterly impossible to say, even approximately. Judging, however, from what we can observe at the present day, the palæontological break between the Chalk and the Eocene indicates a perfectly incalculable lapse of time; for all species change or die out slowly, marine species especially so; and we have here the disappearance of a large fauna almost in its entirety, and its replacement by another wholly distinct.

In the second place, to come to the physical evidence, the Eocene strata in Britain are seen to rest upon an eroded and denuded surface of Chalk, filling up "pipes" and winding hollows which descend far below the general surface of the latter. Not only so, but the base of the Eocene rocks is commonly composed of a bed of rolled and rounded flints, derived from the Chalk, affording incontestable proof that the Chalk had been greatly worn down and removed by denudation before the Eocene beds were deposited upon its surface. In short, the Eocene rocks repose "unconformably" upon the Chalk, and this, as is well known, indicates the following series of phenomena: Firstly, the Chalk was deposited in horizontal layers at the bottom of the Cretaceous sea. Secondly, at some wholly indefinite time after its deposition, after it had become more or less consolidated, the Chalk must have been raised by a gradual process of elevation above the level of the sea, during which it would inevitably suffer vast denudation. Thirdly, after another wholly indefinite period, the Chalk was again submerged beneath the sea, in which process it would be subjected to still further denudation, and an approximately level surface would be formed upon it. Fourthly, strata of Eocene age were deposited upon the denuded surface of the Chalk, filling up all the hollows and inequalities of its eroded surface (fig. 15).

In the unconformability, then, between the Chalk and the Eocene rocks, we have unequivocal evidence—irrespective of anything that we learn from Palæontology—that the break between the two formations was one of enormous length. In Britain the interval of time thus indicated is not represented by any deposits; and in

Europe generally there are but fragmentary traces of such. We may be quite sure, however, that during the time represented in Britain by the mere line of unconformability between the Chalk and the Eocene, there were somewhere deposited considerable accumulations of sediment.

It is not probable that we shall ever discover any very considerable portion of these, considering the large extent of the terrestrial surface which is covered by the ocean. In New Zealand, however,

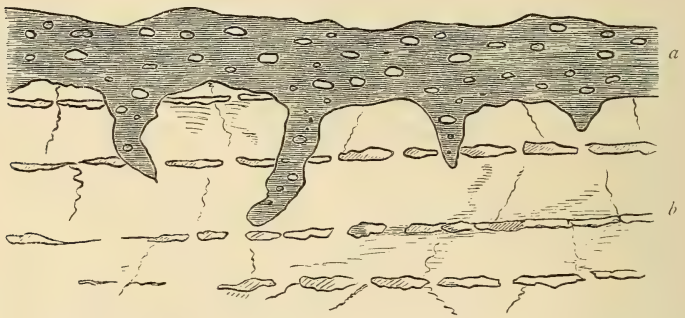


Fig. 15.—Section showing strata of Tertiary age (*a*), resting upon a worn and denuded surface of White Chalk (*b*), the stratification of which is marked by lines of flints.

and still more notably in North America, extensive deposits are already known, which were laid down subsequent to the formation of the White Chalk and prior to the deposition of the Eocene Tertiary, and which serve, therefore, to partially bridge over the great *hiatus* which separates these formations in Europe. These transitional formations are charged, as might have been anticipated, with the remains of animals which in part resemble Cretaceous types and in part are characteristic Eocene forms.

The break between the Cretaceous and lowest Tertiary deposits is one of the most extensive and universal of which we have at present any knowledge. Almost equally extensive and widespread is the break which separates the Palæozoic from the Mesozoic group of deposits. Throughout the whole stratified series, however, we meet at intervals with physical and palæontological breaks of greater or less magnitude. Sometimes a palæontological break occurs unaccompanied by marked physical disturbance or discordance of the strata; but usually a gap in the succession of life-forms is associated with clear physical evidence of elevation and subsequent denudation.

It may be pointed out that the unconformities above alluded to must be distinguished from the common cases in which strata of one age are *locally* superimposed in an unconformable manner upon

beds much older than themselves. These local unconformities are exceedingly common in regions which have undergone much disturbance, and they merely indicate that the region has been subjected to a local elevation, resulting in a temporary cessation of sedimentation in that particular area. In such cases, an examination of neighbouring areas, which remained submerged, and in which, therefore, sedimentation was uninterrupted, will show the missing deposits which were laid down during the period represented in the first area by a local unconformity. The instances above alluded to, though really only differing from the local unconformities just alluded to in nothing more than in being the result of a very widespread elevation, are distinguished by an important point. In the case of a mere local unconformity, we know what formation is wanting, and we can intercalate it from foreign areas, and can thus complete the series. In the general unconformities, such as that between the Palæozoic and Mesozoic groups of sediments, we are not at present acquainted with the deposits which were laid down during the interval represented by the physical discordance of the strata, and the series of rock-formations thus remains a broken one.

From the above facts, then, we learn that one of the chief causes of the imperfection of the palæontological record is to be found in the vast spaces of time which separate most of the great "systems," and which, so far as we yet know, are not represented by any formation of rock. In process of time we shall doubtless succeed in finding deposits to account for more or less of this "unrepresented time," but much will ever remain for which we cannot hope to find the representative sediments. It only remains to add that we have ample evidence within the limits of each formation, and wholly irrespective of any want of conformity, of such lengthened pauses in the work of deposition as to have allowed of great zoological changes in the interim, and to have thus caused irremediable blanks in the palæontological record. The work of rock-deposition is at best an intermittent process; the changes in a fauna, if slowly effected, are continuous. Thus there are scores of instances in which the fauna of a given bed, perhaps but a few inches in thickness, differs altogether from that of the beds immediately above and below, and is characterised by species peculiar to itself. In such cases we can only suppose, that though no physical break can be detected, the deposition of sediment was interrupted by pauses of incalculable length, during which no additional material was added to the sea-bottom, whilst time was allowed for the dying out of old species and the coming in of new. The incessant repetition of such intervals of unrepresented time throughout the whole stratified series is convincing proof that the palæontological record is, and

ever must be, a mere excerpt from the biological annals of the globe.

III. Thinning out of Beds.—Another cause by which the continuity of the palæontological record is affected is what is technically called the "thinning out" of beds. Owing to the mode in which sedimentary rocks are produced, it is certain that there must be for every bed a point whence the largest amount of sediment was derived, and in the neighbourhood of which the bed will therefore be thickest. Thus, if we take a series of beds, such as sandstones and conglomerates, which are the product of littoral action, and are deposited in shallow water near a coast-line, it will be found that these gradually decrease in thickness, or "thin out," as we pass away from the coast in the direction of deep water. On approaching deep water, however, we might find that, though the sandstones were rapidly dying out, the thickness of the entire series might still be preserved, owing to the commencement now of some deep-water deposit, such as limestone. The beds of limestone would at first be very thin, but in proceeding still in the direction of deeper water, we should find that they would gradually expand till they reached a point of maximum thickness, on the other side of which they would

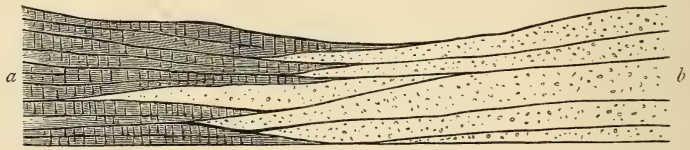


Fig. 16.—Diagram to show the "thinning out" of beds. *a*, Sandstones and Conglomerates; *b*, Limestones.

gradually thin out. Each individual bed, therefore, in any group of stratified rocks, may be regarded as an unequal mass, thickest in the centre, and gradually tapering off or "thinning out" in all directions towards the circumference (fig. 16).

In a general way this holds good, not only for any particular bed, but for any particular aggregation or group of beds which we may choose to take. In the case, namely, of every group of beds, there must have been a particular point whither sediment was most abundantly conveyed, or where the other conditions of accumulation were especially favourable. At this point, therefore, the beds are thickest, and from this they thin out in all directions. It need scarcely be pointed out, indeed, that some such state of things is unavoidable in the case of every bed or group of beds, since no sea is boundless, and the sedimentary deposits of every ocean must come to an end somewhere.

An excellent example of the phenomena above described may be

derived from the Lower Carboniferous rocks of Britain. Here we may start in South Wales and in Central England with the Carboniferous Limestone as a great calcareous mass over 1000 feet in thickness, and almost without a single intercalated layer of shale. Passing northwards, some of the beds of limestone begin to thin out, and their place is taken by strata of a different mineral nature, such as sandstone, grit, or shale. The result of this is, that by the time we have followed the Carboniferous Limestone into Yorkshire and Westmorland, in place of a single great mass of limestone, we have an equivalent mass of alternating strata of limestone, sandstone, grit, and shale, with one or two thin seams of coal—the limestones, however, still bearing a considerable proportion to the whole. Passing still further northwards, the limestones continue to thin out, till in Central Scotland, in place of the dense calcareous accumulations of Derbyshire, the Lower Carboniferous series consists of a great group of sandstones, grits, and shales, with thick and workable beds of coal, and with but few and comparatively insignificant beds of limestone.

The state of things indicated by these phenomena is as follows: The sea in which the Lower Carboniferous rocks of Britain were deposited must have gradually deepened from north to south. The land and coast-line whence the coarser mechanical sediments were derived, must have been placed somewhere to the north and north-west of what is now Great Britain, and the deepest part of the ocean must have been somewhere about Derbyshire. Here the conditions for lime-making were most favourable, and here consequently we find the greatest thickness of calcareous strata, and the smallest intermixture of mechanical deposits.

The palæontological results of this are readily deducible. The entire Lower Carboniferous series of Britain was probably deposited in a single ocean, apparently destitute of land-barriers; and consequently, taken as a whole, the fauna of this series may be regarded as one and indivisible. The conditions, nevertheless, which obtained in different parts of this area were very dissimilar; and, as a necessary result, certain groups of animals flourished in certain localities, and were absent or but scantily represented in others. In the deeper parts of the area we have an abundance of Corals, with Crinoids, and at times *Foraminifera*. In the shallower parts of the area there is, on the other hand, a predominance of forms which affect water of no great depth. Still there is no difference in point of time between the deposits of different parts of the area; and in order to obtain a true notion of the Lower Carboniferous fauna, we must add the fossils derived from one portion of the area to those derived from another.

In many cases, however, we are acquainted with but one class of

deposits belonging to a given period. We may have the comparatively deep-water deposits of the period only, or we may know nothing but its littoral accumulations. In either case it is clear that there is an imperfection of the palæontological record; for we cannot have even a moderately complete record of the marine animals alone of a particular period, unless we have access to a complete series of the deposits laid down in the seas of that period. A still more serious imperfection of the record arises where, as commonly happens, the marine deposits of a given period are alone known, and we are left without any knowledge of the lacustrine, fluviatile, and terrestrial deposits of the same period.

According to the views of Dr John Murray and the Abbé Renard, a very important deficiency exists in the series of sedimentary deposits known to us as forming the existing dry land, in so far as the series is without any representatives of the peculiar deposits which are now in process of formation in the deep sea. It has been shown by these investigators that between depths of six or seven hundred fathoms down to the greatest depths known, at distances of two hundred miles or more from land, there are now being formed certain remarkable deposits which may be spoken of as "deep-sea muds" and "abyssal clays." The deep-sea "muds" and "oozes" are exceedingly fine, mud-like deposits, which differ from true muds in not being made up of water-worn particles of clay or other mineral substances, and in being largely composed of the skeletons of minute animal or vegetable organisms. Some of these deep-sea muds are largely composed of the shells of *Foraminifera* ("Globigerina ooze"); others are essentially made up of the siliceous tests of *Polycystina* and allied organisms ("Radiolarian ooze"); others are built up principally of the shells of *Pteropoda* ("Pteropod ooze"); while others are the result of the accumulation of the flinty envelopes of Diatoms ("Diatom ooze"). The "abyssal clays," again, are red, purple, chocolate-coloured, or brown clays, composed of nearly impalpable particles, and almost destitute of calcareous matter, but sometimes containing particles of metallic iron or concretions of manganese. These abyssal clays, according to Dr Murray, are produced by the decomposition in sea-water of floating pumice and of ashes, ejected from volcanoes and ultimately falling into the sea; and there is evidence to show that they are the result of an excessively slow process of accumulation.

From a study of the deposits at present in process of formation in the deep sea, far from land, it has been concluded by Murray and Renard, as before said, that no similar or parallel deposits exist amongst the varied marine sediments which compose so large a portion of the present continents. On this view, the ordinary stratified rocks of marine origin have all been formed in comparatively shallow water,

or, at any rate, at a comparatively short distance from land. A conclusion so far-reaching as this requires, however, to be received with the utmost caution; the more so as it constitutes one of the most weighty arguments in favour of the equally far-reaching conclusion, that the present continental areas have been in the main regions of elevation, and the existing oceans in the main areas of depression, since the beginning of the Cambrian period, if not from a still earlier period. That a large number of the known sedimentary rocks have been formed from the wear and tear of pre-existing rocks, or have been the result of the accumulation of the skeletons of animals and plants, in comparatively shallow water and at moderate distances from a coast-line, may be taken as certain. With our present imperfect acquaintance, however, with the nature and origin of many of the older sediments of the earth's crust, it appears hazardous to conclude that *all* the sedimentary rocks have been laid down near land. In various parts of the stratified series we meet with deposits which may be paralleled with the Foraminiferal ooze, the Radiolarian ooze, the Diatom ooze, or even the Pteropod ooze of the present day, though it may be admitted that these deposits may sometimes have been formed in a comparatively shallow sea. Moreover, it cannot, with our present knowledge, be safely asserted that we have *no* ancient representatives even of the "abyssal clays" of the deep oceans of the present day. On the contrary, it seems very possible that certain of the sediments of such old systems as the Cambrian and Ordovician were formed at great depths, and that they represent the modern abyssal clays. This is particularly the case with some of the fine-grained, red, brown, or green muds which occasionally form a conspicuous feature in the Cambrian and Ordovician series. Such muds are not only singular for their extraordinary barrenness in fossils, but there is good ground for thinking that they have been formed by the decomposition of volcanic matter, while they commonly exhibit dendrites of manganese.

IV. Disappearance of Fossils.—The last subject which need be mentioned in connection with the imperfection of the palæontological record, is that of the disappearance of fossils from rocks originally fossiliferous. This, as a rule, is due to "metamorphism"—that is to say, the subjection of the rock to a sufficient amount of pressure or heat to cause a rearrangement of its particles. When of at all a pronounced character, the result of metamorphism is the more or less complete obliteration of any fossils which might have been originally present in the rock. To this cause must be set down many great gaps in the palæontological record, and the irreparable loss of much fossil evidence.

Another not uncommon cause of the disappearance of organic remains from originally fossiliferous deposits is the percolation through

them of water holding carbonic acid in solution. By this means fossils of a calcareous nature are dissolved out of the rock, and may leave no traces behind. This cause, however, can only operate to any extent in more or less loose and porous arenaceous deposits.

Lastly, "cleavage" may be mentioned as a common cause of the disappearance of fossils. But the cleavage must be very intense, if it actually prevents the recognition of the deposit as one in which fossils formerly existed, though cases are not uncommon in which this occurs through thousands of feet of strata. As a more general rule, however, it is not very difficult to determine whether a cleaved rock has ever contained fossils or not, though it may be quite impossible to make out the exact nature and character of the organic remains.

CHAPTER V.

CONCLUSIONS TO BE DRAWN FROM FOSSILS.

We have already seen that geologists have been led by the study of fossils to the all-important generalisation that the vast series of the Fossiliferous or Sedimentary rocks may be divided into a number of definite groups or "systems," each of which is characterised by its organic remains. It may simply be repeated here that these systems are not properly and strictly characterised by the occurrence in them of any one particular fossil. It very often happens, indeed, that some particular stratum, or sub-group of a series, contains peculiar fossils, by which its existence may be determined in various localities. As before remarked, however, the great systems are characterised properly by the association of certain fossils, by the predominance of certain families or orders, or by an *assemblage* of fossil remains representing the "life" of the period in which the system was deposited.

Fossils, then, enable us to determine the *age* of the deposits in which they occur. Fossils further enable us to come to very important conclusions as to the mode in which the fossiliferous bed was deposited, and thus as to the condition of the particular district or region occupied by the fossiliferous bed at the time of the formation of the latter. If, in the first place, the bed contain the remains of animals such as now inhabit rivers, we know that it is "fluviatile" in its origin, and that it must at one time have either formed an actual river-bed, or been deposited by the overflowing of an ancient stream. Secondly, if the bed contain the remains of shell-fish, minute crustaceans, or fish, such as now inhabit lakes, we know that it is "lacustrine," and was deposited beneath the waters of a former lake. Thirdly, if the bed contain the remains of animals such as now people the ocean, we know that it is "marine" in its origin, and that it is a fragment of an old sea-bottom.

We can, however, often determine the conditions under which a bed was deposited with greater accuracy than this. If, for example,

the fossils are of kinds resembling the marine animals now inhabiting shallow waters, if they are accompanied by the detached relics of terrestrial organisms, or if they are partially rolled and broken, we may conclude that the fossiliferous deposit was laid down in a shallow sea, in the immediate vicinity of a coast-line, or as an actual shore-deposit. If, again, the remains are those of animals such as now live in the deeper parts of the ocean, and there is a very sparing intermixture of extraneous fossils (such as the bones of birds or quadrupeds, or the remains of plants), we may presume that the deposit is one of deep water. In other cases, we may find, scattered through the rock, and still in their natural position, the valves of shells such as we know at the present day as living buried in the sand or mud of the sea-shore or of estuaries. In other cases, the bed may obviously have been an ancient coral-reef, or an accumulation of social shells, like Oysters. Lastly, if we find the deposit to contain the remains of marine shells, but that these are dwarfed of their fair proportions and distorted in figure, we may conclude that it was laid down in a brackish sea, such as the Baltic, in which the proper saltness was wanting, owing to its receiving an excessive supply of fresh water.

In the preceding, we have been dealing simply with the remains of aquatic animals, and we have seen that certain conclusions can be accurately reached by an examination of these. As regards the determination of the conditions of deposition from the remains of aerial and terrestrial animals, or from plants, there is not such an absolute certainty. The remains of land-animals would, of course, occur in "sub-aerial" deposits—that is, in beds, like blown sand, accumulated upon the land. Most of the remains of land-animals, however, are found in deposits which have been laid down in water, and they owe their present position to having been drowned in rivers or lakes, or carried out to sea by streams. Birds, flying Reptiles, and flying Mammals might also similarly find their way into aqueous deposits; but it is to be remembered that many Birds and Mammals habitually spend a great part of their time in the water, and that these might therefore be naturally expected to present themselves as fossils in Sedimentary rocks. Plants, again, even when undoubtedly such as must have grown on land, do not prove that the bed in which they occur was formed on land. Many of the remains of plants known to us are extraneous to the bed in which they are now found, having reached their present site by falling into lakes or rivers, or being carried out to sea by floods or gales of wind. There are, however, many cases in which plants have undoubtedly grown on the very spot where we now find them. Thus it is now generally admitted that the great coal-fields of the Carboniferous age are the result of the growth *in situ* of the plants which compose coal,

and that these grew on vast marshy or partially submerged tracts of level alluvial land. We have, moreover, distinct evidence of old land-surfaces, both in the Coal-measures and in other cases (as, for instance, in the well-known "dirt-bed" of the Purbeck series). When, for example, we find the erect stumps of trees standing at right angles to the surrounding strata, we know that the surface through which these send their roots was at one time the surface of the dry land, or, in other words, was an ancient soil (fig. 17).

Fig. 17.—Erect Tree containing Reptilian remains. Coal-measures, Nova Scotia. (After Dawson.)

Conclusions as to Climate.—In many cases fossils enable us to come to important conclusions as to the climate of the period in which they lived, but only a few instances of this can be here adduced. As fossils in the majority of instances are the remains of marine animals, it is mostly the temperature of the sea which can alone be determined in this way; and it is important to remember that, owing to the existence of heated currents, the marine climate of a given area does not necessarily imply a correspondingly warm climate in the neighbouring land. Land-climates can only be determined by the remains of land-animals or land-plants, and these are comparatively rare as fossils. It is also important to remember that all conclusions on this head are really based upon the present distribution of animal and vegetable life on the globe, and are therefore liable to be vitiated by the following considerations:—

a. Most fossils are extinct, and it is not certain that the habits and requirements of any extinct animal were exactly similar to, or even at all resembling, those of its nearest living relative.

b. When we get very far back in time, we meet with groups of organisms so unlike anything we know at the present day as to render all conjectures as to climate founded upon their supposed habits more or less uncertain and unsafe.

c. In the case of marine animals, we are as yet very far from knowing the exact limits of distribution of many species within our present seas; so that conclusions drawn from living forms as to extinct species are apt to prove incorrect. For instance, it has

recently been shown that many shells formerly believed to be confined to the arctic seas have, by reason of the extension of polar currents, a wide range to the south; and this has thrown doubt upon the conclusions drawn from fossil shells as to the arctic conditions under which certain beds were supposed to have been deposited.

d. The distribution of animals at the present day is certainly dependent upon other conditions beside climate alone; and the causes which now limit the range of given animals are certainly such as belong to the existing order of things. But the establishment of the present order of things does not date back in many cases to the introduction of the present species of animals. Even in the case, therefore, of existing species of animals, it can often be shown that the past distribution of the species was different formerly to what it is now, not necessarily because the climate has changed, but because of the alteration of other conditions essential to the life of the species or conducing to its extension.

Upon the whole, therefore, it would seem that conclusions as to the climate of any particular area at any given point of geological time must be accepted with considerable caution, unless in cases where there happens to be direct *physical* evidence of an arctic climate. It has, in fact, been even questioned that there existed marked differences in the climate of different regions of the earth in the earlier periods of the earth's history. Rather, it has been held that in ancient geological times an equable temperature reigned over the whole globe, as the result of a relatively high internal terrestrial heat, the earth's surface and the air being thus maintained at a temperature sufficiently high to render the influence of the sun's rays of comparatively little importance. On this view it was supposed that it was only when the earth's internal heat had been largely dissipated by radiation, that climatic zones were developed; the temperature of each region coming ultimately to depend mainly upon the amount of heat which it might receive, directly or indirectly, from the sun. The change from the one condition of things to the other was usually supposed to have corresponded, in a general way, with the commencement of the Tertiary period.

Apart, however, from the inherent improbabilities attaching to this theory—so far, at any rate, as concerns the periods subsequent to the introduction of animal and vegetable life upon the globe—it has been shown by Professor Neumayr that the existence of definite climatic zones can be demonstrated, by the evidence of fossils, in periods at least as ancient as the Jurassic. As regards the Palæozoic period, the principal argument for the assumption that the earth enjoyed a uniformly high temperature, as pointed out by Neumayr, is that the Palæozoic animals, even in northern latitudes,

are often more nearly related to types now living in the tropics than to any others. As regards certain types—such as the ancient and persistent genus *Nautilus*—some weight may be reasonably attached to this argument. Another argument for the assumed uniformity of climate in Palæozoic time may be based upon the extraordinarily wide range in space of many Palæozoic types of animals. Upon the whole, however, the Palæozoic animals differ so widely from their nearest living relatives as to render it very hazardous to base on their supposed habits of life any decided conclusions as to Palæozoic climate. Much the same may be said with regard to the argument in favour of a very uniform and widely spread warm-temperate climate during Carboniferous times, based upon the extension of the predominant Coal-plants to high northern latitudes.

Taken collectively, our knowledge would rather go to show that considerable variations in climate have occurred in all periods subsequent to the appearance of living beings upon the earth. Thus, there is more or less weighty evidence in favour of the occurrence of Glacial periods in various of the older formations, beginning as early as the Cambrian period. In Mesozoic time, certainly, the evidence adduced by Neumayr, Marcou, and Trautschold seems to show conclusively that different regions of the earth enjoyed, as they do at present, different climates. The first of these observers, in particular, has shown that a study of the animal life of the Jurassic deposits of the north hemisphere would support the conclusion that there existed during the Jurassic period three well-marked climatic zones—one boreal, one temperate, and one subtropical—and that two of these, at any rate, can be recognised in the south hemisphere also.

CHAPTER VI.

RELATIONS OF PALÆONTOLOGY TO GEOLOGY AND BIOLOGY—METHODS OF PALÆONTOLOGY—CLASSIFICATION OF THE ANIMAL KINGDOM.

In more than one of its aspects, Palæontology stands in an intimate relation with *Geology*. Thus, so far as it is concerned with investigating the mode of life and distribution in *space* of fossil organisms, Palæontology becomes directly connected with the physiographical side of Geology. From another point of view, in so far as it investigates the relations of fossil organisms to *time*, Palæontology becomes closely interwoven with Historical or Stratigraphical Geology. In all its fundamental aspects, however, Palæontology is essentially a branch of *Biology*—constituting a branch of *Zoology* where it deals with animals, and of *Botany* in so far as it deals with plants. Palæontology, therefore, may be properly divided into the two departments of "Palæozoology" and "Palæobotany." The principal ground for the use of the separate term "Palæontology," as distinct from "Zoology" and "Botany," is simply that in studying extinct organisms we have to take into account *the time at which these lived*. It is therefore the element of time, and that alone, which entitles us to speak of Palæontology as an independent science.

The *methods* of palæontological study are precisely the same as those of Zoology and Botany. It is true that the earlier palæontologists attached a certain importance to the *age* of a fossil, as bearing upon the determination of its affinities, and that it was sometimes assumed that fossils from deposits of different geological ages were necessarily referable to different specific types. At the present day, however, it is recognised that the systematic position and relationships of an extinct organism must be settled by an appeal to its *morphological* characters, altogether or to a great extent irrespective of the age of the deposit in which it occurs. The zoologist and the

botanist similarly rely essentially upon Morphology in the determination of the relations of animals and plants; and there is, therefore, no real difference in the methods of study employed, whether the organisms under examination be living or extinct.

In some respects, however, the zoologist has a great advantage over the palæontologist. The student of living beings can investigate the *entire* organism, the soft parts as well as the hard; and he can also study the "development" of the organism, and by tracing it through its early stages can discover how it came to assume its adult characters. The student of fossil organisms, on the other hand, is restricted, with the rarest exceptions, to an investigation of the *hard parts* only. The conclusions of the palæontologist as to the characters and affinities of fossil animals are necessarily based upon a study of the skeletal structures, from which the characters of the soft parts have to be inferred. Moreover, it commonly happens that even the hard parts of the animal have been imperfectly preserved, and that the object to be studied is a mere fragment of the skeleton, from which all the soft tissues have been removed. Again, it is only in exceptional cases that we have any means of making ourselves acquainted with the development of fossil animals. Considering the generally fragmentary character of the objects with which the palæontologist has to deal, and the almost invariable absence in fossils of any traces of the soft parts of the organism, it might be supposed that the study of fossils was attended with insuperable difficulties. The most serious of these difficulties are, however, overcome by means of the law of the "correlation of organs," the establishment of which by the illustrious Cuvier marks an era in palæontological science.

Stated in its most general form, the law of the correlation of organs is the law that all the parts of an organism stand in some relation to one another, the form and characters of each part being more or less closely dependent on, and connected with, the form and characters of all the rest. In other words, an organism is not a fortuitous collocation of unrelated parts, but is composed of mutually adapted and related organs, the possession of any given organ, therefore, implying the possession of other "correlated" organs. Thus, the possession of mammary glands is "correlated" with the possession of two occipital condyles and of a simple mandible; a stomach adapted for rumination is correlated with the possession of only two functional toes to the foot, and the absence of the central upper incisors; an inflected angle of the lower jaw is usually correlated with the possession of "marsupial bones" or "marsupial cartilages"; a covering of feathers is correlated (in living forms) with saddle-shaped faces to the bodies of the cervical vertebræ. From the above examples it will be evident that, by means of the law of correlation, it

is often possible to infer from an isolated organ or structure the essential characters of the remainder of the organism. Thus, if we were acquainted with no other part of some animal than its skull alone, and if we found that that skull possessed two occipital condyles, and that each half of the lower jaw was composed of a single piece, we should be justified in concluding that the animal to which the skull belonged possessed mammary glands. We should also be justified in inferring many other facts about it, as, for example, that it possessed (or might have possessed) a hairy covering to the body, that its blood was hot, and that it possessed non-nucleated red blood-corpuscles. Similarly, if we met with a mammalian lower jaw, the angle of which was bent inwards, or "inflected," we should have a strong presumption that the animal to which it belonged possessed "marsupial bones" or cartilages on the brim of the pelvis, and that the young were born in a very imperfect state of development. It follows from what has been already said, that the law of the correlation of organs plays a most important part in palæontological investigation, enabling the observer to more or less completely "reconstruct" an extinct organism by means of its fragmentary remains. It is to be remembered, however, that the law is a purely empirical one, and expresses nothing more than the result of experience; so that structures which we now know only as occurring in association may ultimately be found separate, and conjoined with structures of a different character.[1] Moreover, it is to be borne in mind that in any two correlated structures it is not that *each* is correlated with the other, but that *one* of the two is correlated with the other. That is to say, of any two correlated organs, A and B, it may be true that A is never found without B, but it does not follow that B may not occur without A. Thus, the presence of a stomach adapted for "rumination" is invariably associated (in living types) with an imperfect development of the incisors of the upper jaw, the central upper incisors being always wanting; but it is not the case that an incomplete condition of the upper incisors, or the absence of the central ones, is necessarily correlated with the habit of chewing the cud. The proper way of putting the case is to assert that certain structures (A) are never found apart from other structures (B), though the latter may be present without the former. When, therefore, we find a lower jaw having its angle "inflected," we may, with our present knowledge, assert that the animal to which that jaw belonged probably possessed "marsupial bones" or "marsupial cartilages" upon the brim of the pelvis; although the presence of a certain amount of inflection in the jaws of some *Insectivora* would preclude

[1] A remarkable instance where this correlation is at fault, and has led to the reference of the bones of one animal to two distinct orders, will be noticed among the *Mammalia* under the head of *Chalicotherium*.

our making this assertion absolutely positive. If, however, we were to find a pelvis with marsupial bones, we should not be justified in asserting that the owner of the same must have possessed an inflected angle to the lower jaw. On the contrary, we know that such an assertion would be erroneous, since the "marsupial bones" are present in the Monotremes, in which the angle of the jaw has its usual form.

Classification of the Animal Kingdom.

Vast as is the number of known animals, all, whether living or extinct, may be classed under a limited number of primary divisions or "morphological types," which are technically spoken of as the "sub-kingdoms." There are also certain groups of animals (the Molluscoids and Tunicates) which have not the value of "sub-kingdoms," but which are so far separated by their characters from their nearest relatives that it is expedient in the meanwhile to treat them as constituting distinct divisions of the animal kingdom. All the animals in any one sub-kingdom agree with one another in their structural type, or in the fundamental plan upon which they are constructed, and they differ from one another simply in the modifications of this common plan. Two animals belonging to different sub-kingdoms may be rendered closely similar to one another as the result of similar adaptive modifications, but no amount of physiological likeness will counterbalance or efface the morphological unlikeness due to the fact that each is constructed upon an essentially different ground-plan. As the animals belonging to any given sub-kingdom are separated solely by the characters due to varying modifications of a common morphological type, it is possible to arrange the members of each in an approximately linear series, in which the lowest members most closely approach the primitive or ideal form of the sub-kingdom, while the highest exhibit the greatest amount of complexity and specialisation of this type. But it is not possible to establish any such linear classification for the animal kingdom as a whole. Given an animal of a lower "sub-kingdom" than another animal, no amount of complexity, no specialisation of organisation, can raise the former above the latter. The one may be the result of the high evolution of a low morphological type, the other may be the result of the low evolution of a higher morphological type, but the superiority of the ground-plan gives the latter the higher place. It is obvious, therefore, that a linear classification is not possible; since the higher members of each sub-kingdom are more highly organised than the lower forms of the next sub-kingdom in the series, at the same time that they are constructed upon a lower morphological type.

It is, in fact, clear that a pictorial representation of the different groups of the animal kingdom, in the order of their natural alliances, would not exhibit a series of regularly ascending steps, but would have the form of a branched and ramified genealogical tree. Such a tree would exhibit one main stem, which would give origin to numerous lateral stems. These latter would, in turn, subdivide, some branches ascending in the course of their development, while others, as the result of degeneration, would descend.

The terms "class," "order," "genus," "sub-genus," "species," and "variety," are employed by the palæontologist in precisely the same sense, and with precisely the same limitations, as by the zoologist. We must notice, however, that a *palæontological* "species" has not always or necessarily the same value as that which a *zoological* species ought invariably to possess. This arises from the fact that the determination of fossil species is, almost without exception, based solely upon the characters of the hard parts of the animal—these, also, being often but imperfectly preserved. A fossil species, therefore, cannot, from the nature of things, be as thoroughly defined as a living one; and it is both possible and probable that variations in the form of the skeleton, especially if an integumentary one, may often depend upon mere individual, sexual, or local peculiarities, which could be at once discovered in the case of living forms, but which can hardly be detected as regards extinct types. Moreover, there is a practical inconvenience attending the use of the terms "variety" and "sub-genus" in palæontology, which is not found in zoology, owing to the very different nature of the working material of these two sciences. Many palæontologists, therefore, prefer, as we think rightly, to follow the general practice of giving distinct names to "varieties" and "sub-genera," thus practically raising them to the rank of "species" and "genera"; and this practice can hardly be injurious if accompanied with the well-understood reservation that this is done as a matter of convenience only, and that a somewhat wider and looser signification is to be given to the terms "species" and "genus" in palæontology than would be admissible in zoology. At the same time, this practice may be, and has been, carried too far; and in the case of very variable or "protean" species, it is certainly advisable to adhere to the plan usually adopted by British palæontologists—namely, to define the species by its central type, and to group the variable forms under this type as varieties. As a general definition, however, of what is understood in palæontology as a species, we may follow Zittel. This distinguished naturalist defines a palæontological "species" as comprising "all those individuals, or remains of individuals, which possess in common an assemblage of constant characters, and which constitute collectively a distinctly circumscribed morphological series ("For-

menkreis "), apart from all considerations relating to their range in time and in space." Such a series may be connected by transitional forms with other morphological groups without losing its claim to be considered as constituting a "species," provided the series does not shade off in all directions into allied groups.

The following synoptical table gives the leading divisions of the animal kingdom, with typical examples of each. Forms marked with an asterisk are extinct, and are only known in the fossil condition :—

TABULAR VIEW OF THE CHIEF DIVISIONS OF THE ANIMAL KINGDOM.

INVERTEBRATE ANIMALS.

SUB-KINGDOM I.—PROTOZOA.

CLASS I.—GREGARINIDA.

Gregarina, Monocystis. No fossil forms of this class exist.

CLASS II.—RHIZOPODA.

1. MONERA	*Protamœba.* No fossil forms.
2. AMŒBEA	*Amœba, Difflugia, Arcella.* No fossil forms.
3. FORAMINIFERA . . .	*Gromia, Biloculina, Saccammina, Lituola, Textularia, Lagena, Globigerina, Rotalia, * Orbitoides, Nummulina.*
4. RADIOLARIA . . .	*Thalassicolla, Acanthometra, Podocyrtis, Eucyrtidium.*
5. HELIOZOA	*Actinophrys, Actinosphærium.* No fossil forms.

CLASS III.—INFUSORIA.

1. CILIATA	*Paramœcium.* No fossil forms.
2. SUCTORIA	*Acineta.* No fossil forms.
3. FLAGELLATA . . .	*Codosiga.* No fossil forms.
4. CILIO-FLAGELLATA . .	*Ceratium, Peridinium.* Doubtful fossil representatives are known.

SUB-KINGDOM II.—PORIFERA.

CLASS I.—PLETHOSPONGIÆ.

1. MYXOSPONGIÆ . . .	*Halisarca.* No fossil forms.
2. CERATOSPONGIÆ. . .	*Euspongia.* Fossil representatives of doubtful occurrence.
3. MONACTINELLIDÆ . .	*Spongilla, Cliona, * Scoliorhaphis.*
4. TETRACTINELLIDÆ . .	*Tethya, Geodia, Pachastrella, * Tethyopsis.*
5. LITHISTIDÆ . . .	*Discodermia, Corallistes, * Chenendopora, * Doryderma, * Aulocopium, * Siphonia, * Jerea, * Astylospongia.*
6. HEXACTINELLIDÆ . .	*Holtenia, Euplectella, Hyalonema, * Ventriculites, * Protospongia, * Cœloptychium.*

7. *Octactinellidæ . . *Astræospongia.*
8. *Heteractinellidæ . *Tholiasterella, Asteractinella.*

CLASS II.—CALCISPONGIÆ.

1. Homocœla . . . *Leucosolenia.* No fossil forms known. (=*Ascones* of Haeckel).
2. Heterocœla . . . *Grantia, Sycon, *Protosycon* (=*Sycones* of Haeckel), *Leuconia, Leucandra,* &c. (=*Leucones* of Haeckel), **Corynella, **Sestrostomella, *Pharetrospongia* (*Pharetrones*).

SUB-KINGDOM III.—CŒLENTERATA.

CLASS I.—HYDROZOA.

Sub-class I.—Hydroida (Hydroid Zoophytes).

1. Hydrida . . . . *Hydra.* No fossil forms.
2. Corynida . . . . *Coryne, Tubularia, Hydractinia, *Parkeria.*
3. Thecaphora . . . . *Sertularia, Plumularia, Campanularia, *Dendrograptus* (?), **Callograptus* (?).
4. Trachymedusæ . . *Trachynema, Ægina, *Palægina.*

Sub-class II.—Siphonophora.

1. Calycophoridæ . . *Diphyes.* No fossil forms.
2. Physophoridæ . . . *Physalia.* No fossil forms.

Sub-class III.—Lucernarida.

1. Calycozoa . . . . *Lucernaria.* No fossil forms.
2. Acraspeda (Discophora) . *Aurelia, Rhizostoma, *Rhizostomites.*

* Sub-class IV.—Graptolitoidea.

1. Monoprionidæ . . . *Monograptus, Didymograptus, Tetragraptus.*
2. Diprionidæ . . . *Diplograptus, Climacograptus, Retiolites, Phyllograptus.*

Sub-class V.—Hydrocorallinæ.

a. Milleporidæ . . . *Millepora, *Axopora.*
b. Stylasteridæ . . . *Stylaster, Allopora.*
c. *Syringosphæridæ . . *Syringosphæra, Stoliczkaria.*

* Sub-class VI.—Stromatoporoidea.

Stromatopora, Actinostroma, Labechia.

CLASS II.—ACTINOZOA.

1. Zoantharia.
   - *A.* Actiniaria (Zoantharia malacodermata) . . *Actinia.* No fossil forms.
   - *B.* Antipatharia (Zoantharia sclerobasica) . *Antipathes.*
   - *C.* Madreporaria (Zoantharia sclerodermata).
     - *a.* Aporosa . . *Turbinolia, Oculina, Pocillopora, Mæandrina, *Columnaria, *Stauria, *Holocystis, Moseleya.*
     - *b.* Rugosa . . **Cyathophyllum, *Zaphrentis, *Cystiphyllum.*

c. Fungida . . *Fungia*, **Anabacia*.
d. Perforata . . *Madrepora*, *Porites*, **Favosites*, **Syringopora*, **Thecia*.

2. ALCYONARIA
a. Haimeidæ . . . *Monoxenia*, *Hartea*. No fossil forms.
b. Cornulariadæ . . *Cornularia*. No fossil forms.
c. Alcyonidæ . . . *Alcyonium*. No fossil forms.
d. Pseudaxonia . . . *Corallium*, *Mopsea*.
e. Tubiporidæ . . . *Tubipora*. No fossil forms.
f. Helioporidæ . . *Heliopora*.
g. Gorgonidæ . . . *Gorgonia*, *Gorgonella*, *Isis*, *Primnoa*.
h. Pennatulidæ . . . *Pennatula*, **Graphularia*.
i. *Heliolitidæ . . . *Heliolites*, *Plasmopora*.
j. *Halysitidæ . . . *Halysites*.
k. *Tetradiidæ . . . *Tetradium*.
l. *Chætetidæ . . . *Chætetes*.
m. *Auloporidæ . . *Aulopora*, *Cladochonus*.

3. *MONTICULIPOROIDEA. (Zoological affinities uncertain).
a. Monticuliporidæ . . *Monticulipora*.
b. Fistuliporidæ . . *Fistulipora*, *Callopora*.

4. CTENOPHORA . . . *Pleurobrachia*, *Beroe*. No fossil forms.

SUB-KINGDOM IV.—ECHINODERMATA.

DIVISION A.—ECHINOZOA.

CLASS I.—ECHINOIDEA.

1. *PALECHINOIDEA . . *Archæocidaris*, *Bothriocidaris*.
2. EUECHINOIDEA . . . *Echinus*, *Cidaris*, *Spatangus*, **Echinothuria*.

CLASS II.—ASTEROIDEA.

1. *ENCRINASTERIÆ . . *Palæaster*, *Petraster*.
2. ASTERIÆ VERÆ . . . *Asterias*, *Goniaster*, *Solaster*.

CLASS III.—OPHIUROIDEA.

1. EURYALIDA . . . *Asterophyton*, **Onychaster*.
2. OPHIURIDA . . . *Ophioglypha*, **Aspidura*.

CLASS IV.—HOLOTHUROIDEA.

Cucumaria, *Psolus*.

DIVISION B.—PELMATOZOA.

CLASS I.—CRINOIDEA.

1. *PALÆOCRINOIDEA . . *Actinocrinus*, *Cyathocrinus*.
2. NEOCRINOIDEA . . . *Pentacrinus*, **Encrinus*, *Antedon*.

CLASS II.—*CYSTOIDEA.

1. APORITIDÆ . . . *Cryptocrinus*, *Agelacrinus*.
2. DIPLOPORITIDÆ . . . *Glyptosphærites*, *Sphæronites*.
3. RHOMBIFERI . . . *Echinosphærites*, *Caryocrinus*.

CLASS III.—*BLASTOIDEA.

1. REGULARES . . . *Pentremites*, *Granatocrinus*, *Codaster*.
2. IRREGULARES . . . *Astrocrinus*, *Eleutherocrinus*.

SUB-KINGDOM V.—ANNULOSA.

DIVISION I.—SCOLECIDA.

CLASS I.—PLATYELMIA (Flat-worms).

1. TÆNIADA . . . . *Tænia.* No fossil forms.
2. TREMATODA . . . . *Distoma.* No fossil forms.
3. TURBELLARIA . . . *Planaria, Nemertes.* No fossil forms.

CLASS II.—NEMATELMIA (Round-worms).

1. ACANTHOCEPHALA . . *Echinorhynchus.* No fossil forms.
2. GORDIACEA . . . *Gordius.* No fossil forms.
3. NEMATOIDEA . . . *Ascaris.* No fossil forms.

CLASS III.—ROTIFERA (ROTATORIA).

The Wheel-animalcules are wholly unknown in the fossil condition.

DIVISION II.—ANARTHROPODA.

CLASS I.—GEPHYREA (Spoon-worms).

With the very doubtful exception of the Jurassic genus *Epitrachys*, no representative of the Spoon-worms is known in the fossil condition. Well-known recent genera are *Sipunculus* and *Echiurus*.

CLASS II.—MYZOSTOMIDA.

The type-genus is *Myzostoma*. (Recent and fossil).

CLASS III.—ANNELIDA (Ringed-worms).

1. HIRUDINEA . . . *Sanguisuga, Clepsine.* No fossil forms.
2. OLIGOCHÆTA . . . *Lumbricus* (Earth-worm). Not certainly known in the fossil condition.
3. POLYCHÆTA.
   a. Tubicola . . . *Serpula, Spirorbis, *Cornulites.*
   b. Errantia . . . *Nereis, Aphrodite, *Eunicites, *Arabellites.*

CLASS IV.—CHÆTOGNATHA (Arrow-worms).

This class comprises the single recent genus *Sagitta*, and has no fossil representatives.

DIVISION III.—ARTHROPODA.

CLASS I.—CRUSTACEA.

Sub-class I.—Anchoracephala.

1. CIRRIPEDIA . . . *Lepas* (Barnacle), *Balanus* (Acorn-shell), **Turrilepas.*
2. RHIZOCEPHALA . . . *Peltogaster, Sacculina.* No fossil forms.

Sub-class II.—Entomostraca.

1. OSTRACODA . . . *Cypris, Cypridina, *Beyrichia, *Primitia.*
2. COPEPODA . . . . *Cyclops, Lernæa, Argulus.* No fossil forms.
3. CLADOCERA . . . *Daphnia.* No fossil forms.
4. PHYLLOPODA . . . *Apus, Estheria, Branchipus.*
5. PHYLLOCARIDA . . . *Nebalia, *Hymenocaris, *Ceratiocaris, *Discinocaris.*

Gigantostraca
6. *Trilobita . . *Asaphus, Calymene, Illænus.*
7. Xiphosura . . *Limulus* (King-crab), **Belinurus.*
8. *Eurypterida . . *Eurypterus, Pterygotus.*

Sub-class III.—Malacostraca.

1. Amphipoda . . . *Talitrus, Gammarus, *Prosoponiscus.*
2. Isopoda . . . . *Idotea, Oniscus, Serolis, *Archæoniscus.*
3. Stomatopoda . . . *Squilla* (Locust-shrimp).
4. Schizopoda . . . *Mysis* (Opossum-shrimp).
5. Cumacea . . . . *Diastylis.*
6. Decapoda.
   a. Macrura . . . *Homarus* (Lobster).
   b. Anomura . . . *Pagurus* (Hermit-crab).
   c. Brachyura . . . *Cancer* (Crab).

CLASS II.—ARACHNIDA.

1. Podosomata (Pycnogonida) *Pycnogonum, Nymphon.* No fossil forms.
2. *Anthracomarti . . *Arthrolycosa, Architarbus, Anthracomartus.*
3. Acarina . . . . *Acarus, Ixodes, Hydrachna.*
4. Adelarthrosomata . . *Phalangium, Chelifer, Galeodes.*
5. Pedipalpi . . . . *Scorpio, *Palæophonus, *Proscorpius.*
6. Araneida . . . . *Tegenaria, Epeira, *Protolycosa.*

CLASS III.—MYRIOPODA.

1. Onychophora . . . *Peripatus.* No fossil forms.
2. Pauropoda . . . *Pauropus.* No fossil forms.
3. *Protosyngnatha . . *Palæocampa.*
4. Chilopoda . . . . *Scolopendra, Lithobius, Geophilus.*
5. *Archipolypoda . . *Archidesmus, Euphoberia, Archiulus, Xylobius.*
6. Diplopoda (Chilognatha) *Iulus, Polydesmus.*

CLASS IV.—INSECTA.

1. Anoplura . . . *Pediculus.* No fossil forms.
2. Mallophaga . . . *Trichodectes.* No fossil forms.
3. Collembola . . . *Podura.*
4. Thysanura . . . *Lepisma, Petrobius.*
5. *Palæodictyoptera . *Eugereon, Dictyoneura, Palæoblattina.*
6. Rhynchota (Hemiptera) *Nepa, Cicada, Notonecta.*
7. Othoptera . . . *Blatta, Mantis, Gryllus, Œdipoda, Forficula.*
8. Neuroptera.
   a. Pseudoneuroptera . *Libellula, Termes, Ephemera.*
   b. Neuroptera Vera . *Myrmeleon, Hemerobius, Panorpa.*
   c. Trichoptera . . *Phryganea, Limnophilus.*
9. Aphaniptera . . . *Pulex.* No fossil forms.
10. Diptera . . . . *Culex, Musca, Tipula.*
11. Lepidoptera . . . *Vanessa, Sphinx, Bombyx.*
12. Hymenoptera . . . *Apis, Vespa, Formica.*
13. Strepsiptera . . . *Stylops, *Triæna.*
14. Coleoptera . . . *Melolontha, Carabus, Cicindela.*

MOLLUSCOIDEA.

CLASS I.—POLYZOA.

Sub-class I.—Ectoprocta.

1. Phylactolæmata . . *Plumatella.* No fossil forms.
2. Gymnolæmata.
   a. Cyclostomata . . *Tubulipora, Diastopora, *Fenestella, *Ptilodictya.*

b. Cheilostomata . . . *Cellepora, Eschara, Lepralia, Flustra, Bugula.*
c. Ctenostomata . . *Vesicularia, Alcyonidium.* No fossil forms.

Sub-class II.—Entoprocta.

Loxosoma, Pedicellina. No fossil forms.

Sub-class III.—Aspidophora.

Rhabdopleura. No fossil forms.

CLASS II.—BRACHIOPODA.

1. INARTICULATA . . . *Crania, Discina, Lingula, * Lingulella, * Acrotreta.*
2. ARTICULATA . . . *Terebratula, Rhynchonella, *Spirifera, *Strophomena, * Orthis, * Producta.*

SUB-KINGDOM VI.—MOLLUSCA.

CLASS I.—LAMELLIBRANCHIATA (CONCHIFERA or PELECYPODA).

1. OSTREACEA . . . *Ostrea, * Gryphæa, Anomia.*
2. PECTINACEA . . . *Spondylus, Lima, Pecten.*
3. MYTILACEA . . . *Avicula, * Aviculopecten, Mytilus, Pinna.*
4. ARCACEA . . . . *Arca, Pectunculus, Nucula.*
5. SUBMYTILACEA . . . ** Modiolopsis, Trigonia, Unio, Astarte, Crassatella.*
6. ERYCINACEA . . . ** Erycina, Galeomma.*
7. CARDIACEA . . . *Tridacna, Cardium, * Lunulicardium.*
8. CHAMACEA . . . *Chama, * Diceras, * Caprina, * Hippurites.*
9. CONCHACEA . . . ** Megalodon, Cyprina, Venus, Cyrena, Psammobia, Solen, Donax.*
10. MYACEA . . . . *Mactra, Mya, Glycimeris, Gastrochæna.*
11. ADESMACEA . . . *Pholas, Teredo.*
12. LUCINACEA . . . *Lucina, Corbis.*
13. TELLLINACEA . . . *Tellina, Scrobicularia.*
14. ANATINACEA . . . *Solemya, Anatina, Pholadomya, Clavagella.*

CLASS II.—GASTROPODA.

Sub-Class I.—Branchiogastropoda.

1. PROSOBRANCHIATA . . *Buccinum, Strombus, Littorina, Natica, *Murchisonia.*
2. OPISTHOBRANCHIATA . . *Actæon, Bulla, Aplysia, Doris.*
3. PTEROPODA.
   a. Gymnosomata . . *Clio, Pneumodermon.* No fossil forms.
   b. Thecosomata . . *Cavolinia, Cleodora, * Hyolithes, * Tentaculites.*
4. HETEROPODA . . . *Carinaria, Atlanta.*

Sub-class II.—Pulmogastropoda.

1. STYLOMMATOPHORA . . *Helix, Limax.*
2. BASOMMATOPHORA . . *Limnæa, Planorbis.*

CLASS III.—POLYPLACOPHORA.

1. CHITONIDÆ . . . *Chiton, * Helminthochiton.*

CLASS IV.—SCAPHOPODA.

1. SOLENOCONCHIA . . . *Dentalium.*

CLASS V.—CEPHALOPODA.

1. DIBRANCHIATA . . . *Loligo, Sepia, Spirula, Octopus, *Belemnites.*
2. TETRABRANCHIATA . . *Nautilus, *Orthoceras, *Ammonites, *Baculites.*

TUNICATA.

[The Tunicates or Ascidians occupy a position intermediate between *Mollusca* and *Vertebrata*. No fossil forms are known, except in late Tertiary deposits.]

VERTEBRATE ANIMALS.[1]

SUB-KINGDOM VII.—VERTEBRATA.

CLASS I.—LEPTOCARDIA.

PHARYNGOBRANCHEI . . *Branchiostoma* (*Amphioxus*). No fossil forms.

CLASS II.—PISCES (FISHES).

1. CYCLOSTOMI (MARSIPOBRANCHII . . . . *Myxine, Petromyzon.* No fossil forms.
2. ELASMOBRANCHEI.
   - *a.* *Ichthyotomi . . *Pleuracanthus.*
   - *b.* Selachii
     - (1) Tectospondyli . *Cestracion, Lamna, Spinax.*
     - (2) Asterospondyli . *Squatina, Raia.*
3. CHIMÆROIDEI . . . *Chimæra, *Ischiodus.*
4. DIPNOI . . . . *Lepidosiren, Ceratodus.*
5. GANOIDEI.
   - *a.* *Cephalaspidea . . *Cephalaspis, Pteraspis.*
   - *b.* *Placodermata . . *Pterichthys, Coccosteus.*
   - *c.* *Acanthodea . . *Acanthodes, Diplacanthus.*
   - *d.* Crossopterygea . . **Holoptychius, Polypterus.*
   - *e.* Acipenseroidea .. . *Acipenser, *Palæoniscus.*
   - *f.* Lepidosteoidea . . *Lepidosteus, *Dapedius.*
   - *g.* Amioidea . . . *Amia, *Caturus.*
6. TELEOSTEI.
   - *a.* Physostomi . . . *Salmo, Esox, Silurus.*
   - *b.* Anacanthini . . . *Gadus, Rhombus.*
   - *c.* Pharyngognathi . . *Labrax, *Phyllodus.*
   - *d.* Acanthopterygii . . *Mugil, Perca.*
   - *e.* Lophobranchii . . *Solenostoma, Hippocampus.*
   - *f.* Plectognathi . . . *Balistes, Diodon.*

CLASS III.—AMPHIBIA (AMPHIBIANS).

1. *LABYRINTHODONTIA.
   - *a.* Branchiosauria . . *Protriton.*
   - *b.* Æstopoda . . . *Dolichosoma, Ophiderpeton.*
   - *c.* Microsauria . . . *Urocordylus, Ceraterpeton.*
   - *d.* Labyrinthodontia Vera . *Archegosaurus, Mastodonsaurus.*

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[1] The classification of Vertebrate Animals here followed is, in the main, the one which has been adopted in the latest of the Catalogues of fossil Vertebrates issued by the Trustees of the British Museum.

2. APODA (OPHIOMORPHA) . . *Cæcilia, Siphonops.* No fossil forms.
3. CAUDATA (URODELA) . . *Molge, Megalobatrachus.*
4. ECAUDATA (ANOURA) . . *Rana, Bufo.*

CLASS IV.—REPTILIA (REPTILES).

1. * ANOMODONTIA.
   - *a.* Pariasauria . . *Pariasaurus, Pariotichus.*
   - *b.* Theriodontia . . *Galesaurus, Clepsydrops.*
   - *c.* Dicynodontia . . *Dicynodon, Oudenodon.*
   - *Group* Placodontia . . *Placodus, Cyamodus.*
2. * SAUROPTERYGIA . . *Plesiosaurus, Pliosaurus, Nothosaurus, Lariosaurus.*
3. CHELONIA.
   - *a.* Athecata . . . *Dermatochelys, * Protostega.*
   - *b.* Testudinata or Thecaphora . . . *Testudo, Chelone, Trionyx, Chitra, Emyda.*
4. * ICHTHYOPTERYGIA . . *Ichthyosaurus, Baptanodon.*
5. * PROTEROSAURIA . . *Proterosaurus.*
6. RHYNCHOCEPHALIA.
   - * *a.* Simædosauria . . *Champsosaurus.*
   - *b.* Sphenodontina . . *Sphenodon, * Hyperodapedon.*
   - * *c.* Homæosauria . . *Homæosaurus, Sapheosaurus.*
7. SQUAMATA.
   - *a.* Lacertilia . . . *Lacerta, Varanus.*
   - *b.* Rhiptoglossa . . *Chamæleon.*
   - *c.* * Dolichosauria . . *Dolichosaurus.*
   - *d.* * Pythonomorpha . *Clidastes, Mosasaurus.*
   - *e.* Ophidia . . . *Python, Coluber, Vipera.*
8. * DINOSAURIA.
   - *a.* Ornithopoda . . *Iguanodon, Scelidosaurus.*
   - *b.* Theropoda . . . *Megalosaurus, Zanclodon.*
   - *c.* Sauropoda . . . *Ornithopsis, Diplodocus.*
9. CROCODILIA.
   - *a.* * Aëtosauria . . *Aëtosaurus.*
   - *b.* * Parasuchia . . *Parasuchus, Stagonolepis.*
   - *c.* Eusuchia . . . *Crocodilus, * Steneosaurus.*
10. * ORNITHOSAURIA.
    - *a.* Pterosauria . . . *Pterodactylus, Rhamphorhynchus.*
    - *b.* Pteranodontia . . *Pteranodon.*

CLASS V.—AVES (BIRDS).

1. * SAURURÆ . . . *Archæopteryx.*
2. RATITÆ.
   - *a.* * Odontolcæ . . *Hesperornis.*
   - *b.* * Æpyornithes . . *Æpyornis.*
   - *c.* Apteryges . . . *Apteryx, * Megapteryx.*
   - *d.* * Immanes . . . *Dinornis, Palapteryx.*
   - *e.* Megistanes . . . *Casuarius, Dromæus.*
   - *f.* Rheæ . . . . *Rhea.*
   - *g.* Struthiones . . . *Struthio.*
   - *h.* Gastornithes . . *Gastornis.*
3. CARINATÆ.
   - *a.* * Odontotormæ . . *Ichthyornis.*
   - *b.* Crypturi . . . *Tinamus.* No fossil forms.
   - *c.* Impennes . . . *Aptenodytes, * Paleudyptes.*
   - *d.* Tubinares . . . *Procellaria, Puffinus.*
   - *e.* Pygopodes . . . *Alca, Colymbus.*
   - *f.* Gaviæ . . . . *Larus.*

g. Limicolæ . . . *Limicola, Scolopax.*
h. Alectorides . . . *Grus, Otis.*
i. Fulicariæ . . . *Rallus, Notornis.*
j. Gallinæ . . . *Gallus, Crax.*
k. Columbæ . . . *Columba, Pterocles, * Didus.*
l. Anseres . . . *Anser, Anas.*
m. Palamedeæ . . . *Chauna.* No fossil forms.
n. Odontoglossi . . *Phœnicopterus, * Elornis.*
o. Herodiones . . . *Ciconia, Ardea.*
p. Steganopodes . . *Phalacrocorax, Diomedea.*
q. Accipitres . . . *Aquila, Vultur.*
r. Striges . . . . *Otus, Nyctea.*
s. Psittaci . . . . *Psittacus, Cacatua.*
t. Picariæ . . . . *Picus, Cuculus.*
u. Passeres . . . *Passer, Corvus.*

CLASS VI.—MAMMALIA (MAMMALS).

Sub-class I.—Prototheria.

1. MONOTREMATA . . . *Ornithorhynchus, Echidna.*

Sub-class II.—Metatheria.

1. MARSUPIALIA.
   a. Polyprotodontia . . *Dasyurus, Perameles.*
   b. Diprotodontia . . *Macropus, Phascolemys.*

Sub-class III.—Eutheria.

1. EDENTATA . . . . *Cholœpus, Manis, Dasypus.*
2. CETACEA.
   a. Odontoceti . . . *Delphinus, Physeter.*
   b. * Archæoceti . . . *Zeuglodon.*
   c. Mystacoceti . . . *Balæna, Balænoptera.*
3. SIRENIA . . . . *Halicore, Manatus.*
4. UNGULATA.
   a. Artiodactyla . . . *Sus, Cervus, Bos.*
   b. Perissodactyla . . *Rhinoceros, Tapirus, Equus.*
   c. * Toxodontia . . . *Toxodon, Typotherium.*
   d. * Condylarthra . . *Periptychus, Phenacodus.*
   e. Hyracoidea . . . *Hyrax.* No fossil forms.
   f. * Amblypoda . . *Coryphodon, Dinoceras.*
   g. Proboscidea . . . *Elephas, * Dinotherium.*
   Group * Tillodontia . . *Tillotherium.*
5. RODENTIA.
   a. Duplicidentata . . *Lepus, Lagomys.*
   b. Simplicidentata . . *Mus, Sciurus, Hystrix.*
6. CARNIVORA.
   a. Pinnipedia . . . *Phoca, Otaria.*
   b. Carnivora Vera . . *Felis, Ursus, Mustela.*
   c. * Creodonta . . . *Hyænodon, Pterodon.*
7. INSECTIVORA.
   a. Insectivora Vera . . *Talpa, Erinaceus.*
   b. Dermoptera . . . *Galeopithecus.* No fossil forms.
8. CHIROPTERA.
   a. Microchiroptera . . *Vespertilio, Rhinolophus.*
   b. Megachiroptera . . *Pteropus.* No fossil forms.
9. PRIMATES.
   a. Lemuroidea . . . *Lemur, Indris.*
   b. Anthropoidea . . *Macacus, Simia.*

CHAPTER VII.

THE EVOLUTION OF ORGANIC TYPES IN TIME.

The naturalists of last century, and of the earlier part of this century, generally believed that the existing forms of animals and plants had been simultaneously produced by a special act of creation, and that they had not been preceded by pre-existent animals and plants. The occurrence of fossils in the crust of the earth had, it is true, been for long recognised, and had given rise to much learned controversy. By some, fossils were looked upon as having been produced by inorganic agencies, and thus as not being really the remains of animals and plants. Others, again, clearly recognised that fossils were truly the remains of organisms, but regarded them as having belonged to animals that had been destroyed in the Noachian deluge.

At the present day it is universally recognised that our existing animals and plants have been preceded by many antecedent faunæ and floræ. It is also generally admitted that the existing animals and plants are the modified descendants of older forms of life. The actual *beginnings* of life upon the earth are still unknown to us, and are likely ever to remain so. We have no reason to think that the most ancient of known fossils belong to the animals which first came into existence, but much reason to come to an opposite conclusion. Palæontology teaches us that new forms of life have been from time to time introduced upon the earth, and that forms already in existence have become extinct. The laws which have governed this introduction of new and disappearance of old life-forms are still imperfectly known to us, but of the *fact* of this succession of organic types in time no doubt whatever is possible. It is also quite certain that there has been not only a *succession* but likewise a *progression* of organic forms in proceeding from the most ancient of geological periods to the present day. The whole subject of the evolution of life-forms in time involves some of the most profound problems of Palæontology, and can be but very briefly glanced at here. The more im-

portant points in connection with this subject may, however, be shortly considered under the following heads :—

1. *The Primordial Types of Life.*—As above remarked, we know nothing, and are never likely to know anything, of the animals and plants which really constituted the first living beings. Of the life of the Archæan period we at present have no certain knowledge ; but we find representatives of all the Invertebrate sub-kingdoms in the earliest fossiliferous deposits (Cambrian and Ordovician), while Vertebrates appear low down in the Silurian (in the Clinton formation of North America). It may, however, be taken as certain that these ancient fossils cannot possibly be the remains of the really primordial forms of life. Thus, regarded as individuals, these old organic types are as complex and as highly specialised in their structure as are the animals now in existence. Moreover, the great Invertebrate groups of the *Annulosa* and *Mollusca* are found in the Cambrian period to be represented by many diverse forms, and to have already reached a stage of advanced development. It would, however, be at variance with all that we learn from the study of existing organisms, that these great morphological types should, to begin with, have presented themselves under highly specialised forms. Rather must we conclude that a very long period must have been required for the evolution of these varied morphological types, and that the Cambrian fauna was really preceded by many antecedent faunæ which are at present unknown to us.

2. *The Introduction of New Species.*—From the beginning of the Cambrian period onwards, new species of animals have been introduced upon the earth, apparently almost continuously. We may certainly say that the introduction of new species has been "continuous," if we use this term in the sense "of the continued operation of the cause or causes which introduced life at first" (Dawson). It has long been recognised that at certain periods in geological history large numbers of new species were introduced, and this was formerly explained on the supposition that life was periodically destroyed by physical convulsions, and that each of these "catastrophes" was followed by a creation of new animals and plants. The apparent periodicity in the introduction of new species is, however, probably really due simply to the imperfection of the geological record. In all those cases, therefore, where we meet with the apparently sudden incoming of a large number of new life-forms, we may take it for granted that we have to deal with a hiatus in the geological record in the particular area in which this phenomenon is observed. The new forms have, namely, been in existence elsewhere, and what we are observing is not their first introduction upon the earth, but merely their first introduction into the area in question. As regards the period in which we are now living, any apparent ces-

sation in the introduction of new species is probably mainly due to the shortness of the period during which accurate observations have been carried on. Moreover, though our present species have existed for a time which, relatively to man, is very long, this time, estimated geologically, may be, and probably is, very short. It is, further, exceedingly probable that the introduction of new species would, under any circumstances, be imperceptible to a single observer, or even to many successive generations of observers, since the changes by which species are evolved from pre-existing species are probably so slowly produced as to be imperceptible except when fully completed.

3. *Abrupt Appearance of New Species.*—In a large number of instances new morphological types appear to have come into existence abruptly, no closely allied types being known to have preceded them. This is necessarily the case with the animals of the most ancient of the fossiliferous formations (viz., the Lower Cambrian); but a similar phenomenon is observable in hosts of other instances, where we might reasonably expect to find that the new types were preceded by older relatives. It is obvious, however, that this apparently abrupt appearance of a new morphological type—as, for example, the sudden appearance of the great family of the *Rudistæ* in the Cretaceous period—arises from an imperfection in our knowledge. On any theory of evolution, each morphological type must have come into existence, coincidently, both in space and time, with a pre-existing allied morphological type (Wallace). When, therefore, we find new morphological types suddenly appearing on a given geological horizon, in an area where no allied forms have been found in older deposits, we must come to one or other of two conclusions. Either the apparent absence of allied types in older strata is due to the fact that these strata have not been sufficiently investigated, or the apparently sudden introduction of the new forms is due to the fact that the case is not one of their first coming into existence at all, but simply one of their first appearance in the area under observation. In many instances where new organic types suddenly appear in an area, the older deposits in which we might expect to find the remains of the predecessors of these, are missing altogether in the same area. Thus, we cannot expect to find the immediate predecessors of the numerous new life-forms which in Europe usher in the commence ment of the Secondary period, till we find the deposits which were laid down in the interval between the close of the Permian and the beginning of the Triassic period. In many other instances, however, where the series of the stratified deposits may be moderately complete, the apparent abruptness of appearance of a given morphological type is really due to the fact that the series has been imperfectly examined; and further investigation would either show that the type in question really began to exist at an earlier period, or

would bring to light allied types from which we might suppose it to have descended.

4. *Relative Persistence of Species in Time.*—The duration in time, or "vertical range" of species, varies greatly in different cases. Some species have an extraordinarily extended range, sometimes passing through two or three geological systems, and in such cases they generally exhibit numerous varieties. This is the case, for example, with some of the Brachiopods, such as *Strophomena rhomboidalis* and *Atrypa reticularis*. Others, again, are singularly restricted in their range, and do not pass beyond the limits of a single subdivision of a system, or, it may be, even of a single band or zone. No case is known in which a species which has once fairly died out has re-appeared at a later period, but there is no absolute impossibility in the separate evolution of the same specific type at two separate periods. As a general rule, it is the animals which have the lowest and simplest organisation that have the longest range in time, and the additional possession of microscopic or minute dimensions seems also to favour longevity. Some of the *Foraminifera*, for example (*e.g.*, *Saccammina Carteri*), seem to have survived, with little or no perceptible alteration, from the Ordovician period to the present day. On the other hand, large and highly organised animals, though long-lived as *individuals*, rarely seem to live long as *species*, and have, therefore, usually a restricted vertical range. Some *genera*, as some species, are short-lived; whereas others extend through a succession of geological periods with extraordinarily little modification. Among these "persistent types" may be specially mentioned the genus *Lingula* among the Brachiopods, and *Nautilus* (in the wide sense of the name) among the Cephalopods, of which the former commenced in the Cambrian and the latter in the Ordovician, and both of which are represented by living species.

5. *Relative Range of Morphological Types in Space.*—The range of particular morphological types in space is as variable as it is in time. Some forms appear to be wholly restricted to some particular area, or, possibly, to a single locality; while others have an enormous range, and are found at very widely distant points of the earth's surface. In a general way, the types which have a wide range in *time* have also a wide range in space. Thus, species of Brachiopods like *Strophomena rhomboidalis* and *Atrypa reticularis*, which range through more than one geological system, have likewise a very extended geographical distribution. Still, a species which is confined to a single system may have an enormous range in space—as, for example, the common *Producta semireticulata* of the Lower Carboniferous; while in some cases types which are restricted to a single "zone," like certain Graptolites and Ammonites, are found to range over very wide areas. The apparently simultaneous appear-

ance of *groups* of morphological types in corresponding geological periods in widely separated areas of the earth's surface is probably fallacious. Such groups must have appeared first in one area, and their extension therefrom must have been the result of subsequent migration. The only other explanation of this phenomenon would be that the same morphological types had been *simultaneously* produced at several widely remote points; but this hypothesis is apparently irreconcilable with any theory of evolution.

6. *Extinction of Morphological Types.*—While new species have been constantly appearing throughout geological time, old species have as constantly been undergoing extinction. In some cases, extinction seems to have taken place with extraordinary abruptness, as seen, for example, in the sudden disappearance of the *Rudistæ* at the close of the Cretaceous period. In other cases, extinction has been a gradual process. In either case, we are to a large extent ignorant of the causes of extinction, and of the laws under which the process is carried on. As a general rule, it may be taken for granted that the sudden disappearance of a whole group of morphological types is more apparent than real. When we have a sufficiently complete series of deposits, it is usual to find that a group has begun to dwindle down long before it finally disappears from the scene. Thus, the Graptolites, the Trilobites, and the Orthoceratites exhibit a progressive diminution as regards the number of specific types before we reach the point at which extinction takes place. *Why* these, and other similar groups, should show such an extraordinary power of rapid extension and of the development of new specific or generic types when first introduced upon the earth, and should thereafter progressively decay and ultimately become extinct, is a problem for which the solution has yet to be found. In any case, it is to be remembered that in many cases "extinction" implies nothing more than continued existence under a new form. That is to say, a species often becomes apparently extinct by becoming gradually modified into a new species, in which case the parent-form actually disappears, but the modified form represents it in later deposits.

7. *Evolution of Morphological Types from pre-existing Forms.*—Palæontology has furnished a mass of evidence in favour of the view that the introduction of new species in past time has been by evolution from pre-existing forms. Taken as a whole, therefore, the evidence of Palæontology points to the operation of some general law of evolution, whereby the later forms of life have been derived from the older ones. The principal palæontological facts which support the general theory of the evolution of organic types from pre-existing forms may be briefly glanced at here under the following heads :—

(*a.*) In the first place, it is a powerful argument in favour of the theory of evolution that the primary morphological types which we recognise among existing animals are identical with the types upon which fossil animals are constructed. While the great majority of fossils are extinct, and while many of them are extremely unlike any existing forms, no fossil animal has hitherto been detected which cannot be referred to one or other of the existing *sub-kingdoms*. Few fossil animals, indeed, possess peculiarities so great as to entitle them to be placed in any *class*, other than in one of the classes of recent forms. On the other hand, the differences between some of the ancient types of life and the existing ones are so great, that palæontologists have been compelled to construct new *sub-classes*, *orders*, and *genera* for their reception.

(*b.*) Again, the investigation of fossil animals has tended to greatly diminish the intervals by which allied groups of existing animals are separated. Many fossil animals, namely, are what has been termed "comprehensive" in their morphological characters. That is to say, they combine in themselves structural peculiarities which in later formations or at the present day are only found separately, in groups more or less widely removed from one another. These "synthetic types" or "collective types" serve to bridge over the gaps between related morphological types, and are thus of special interest from a theoretical point of view. Thus, to take a single example only, the two great classes of the *Sauropsida*—viz., the Reptiles and the Birds—are at the present day separated by a wide interval. Palæontology, however, has brought to light a number of transitional fossil forms—some referable to Birds and some to Reptiles—which more or less markedly combine in themselves the distinctive characters of both groups, and thus partially fill up the gap which now exists between these two great divisions of Vertebrates.

(*c.*) Again, many fossil animals exhibit what are termed "generalised" characters. If, namely, we construct for ourselves a "general" or "ideal" *type* for any great group of animals—a type which shall possess all the essential characters of the group, without its non-essential ones—then we find that the fossil animals of the same group are generally nearer to this type than are its living representatives. Moreover, the older representatives of any given group are usually nearer to the ideal type of the group—or are more "generalised"—than are the later representatives of the same group. All zoologists, however, admit that the process of development in any individual animal is one in which there is a gradual progress from the general to the special, the embryo being nearer to the general type of the group to which it belongs than the adult is. In other words, the embryo animal is more *generalised* than the adult, and the process of development is one of *specialisation*. Admitting this,

it follows that the fossil forms belonging to any given group, in so far as they are "generalised" in their characters, may fairly be said to be "embryonic" types; and as the oldest forms of any given group are usually the least specialised, so they are likewise the most "embryonic." It must be borne in mind, however, that if we speak of fossil animals as being "embryonic types," we can only do so on the distinct understanding that it is not thereby implied that they were in any way degraded forms, or that they were at all less perfectly constructed, or less thoroughly adapted for their surroundings, than their modern representatives.

(*d.*) Lastly, overwhelming evidence in favour of a general theory of evolution is afforded by the similarity of the types of life in successive faunæ and floræ. The animals and plants of each geological system are more closely related to the animals and plants of the system immediately below and to those of the system immediately above, than they are to the organisms of any other rock-group in the stratified series. This fundamental palæontological fact does not admit of reasonable explanation except upon the view that the organisms of each geological period are the modified descendants of those of the preceding period, and are the progenitors of the organisms of the next succeeding period. Each geological system has, of course, more or fewer special types of life, which are confined to it, and which, apparently from inability to adapt themselves to changes in their environment, die out before the close of the system without leaving descendants. Others undergo but slight modification, and appear in the next system as new species, "representative" of the species from which they sprang. Others, again, vary more profoundly, and break up into diverging groups, represented in the succeeding period by more or less widely distinct forms.

8. *General Progression of Organic Types.*—The history of living forms, as preserved in the palæontological record, exhibits a distinct upward progress from the lower to the higher, or from the more generalised to the more specialised. At the present day, the animal kingdom admits of division into a number of primary morphological types, of which some are higher than others. Thus, the Vertebrate type is zoologically higher than any type of the Invertebrates, and the sub-kingdoms of the latter have also a certain relative rank according to the complexity of their plan of organisation. In the same way, within the limits of each sub-kingdom, some of the groups are more "specialised," and therefore higher in the scale, than others.

Not only do the primary morphological types differ from one another in relative zoological rank, as estimated by relative complexity of organic plan, but Palæontology shows clearly that there has been a *progression* in the order of their development, the lower types having, in the main, preceded the higher in time. It is true, as before

pointed out, that it is very doubtful if we are as yet acquainted with the *absolute* time of the first appearance upon the globe of even one of the sub-kingdoms. Future discoveries, therefore, are almost certain to push back still further into the remote vistas of the past the point of time at which each morphological type first made its appearance upon the globe. Nevertheless, there is little likelihood that the *relative* times of appearance of the great groups, as compared with one another, will be affected by any discoveries which we have yet to make. Moreover, as regards the Invertebrate sub-kingdoms, we are, perhaps, never likely to find any reliable evidence which would enable us to fix with precision their relative order of appearance. All of these sub-kingdoms appear in the Cambrian deposits, and the utmost that we can be certain of is that they had been in existence in times long anterior to the Cambrian. Owing, however, to the very general metamorphism which has affected the pre-Cambrian sediments, we cannot hope to ever obtain more than the most scanty evidence, if any, as to the actual origin of the earliest types of life. With regard to the Vertebrate animals, on the other hand, the series of the fossiliferous rocks is long enough to render it certain that within its limits we ought to find traces of the first appearance of, at any rate, the higher classes of these, though we are doubtless likely to remain ignorant of the precise stage in the series at which each first made its appearance. If, therefore, it can be shown that there has been a progression so far as this sub-kingdom is concerned, then there would, by analogy, be the greatest probability that a similar progression has taken place as regards all the sub-kingdoms.

So far as our present knowledge goes, it would appear certain that there *is* such a progression in the Vertebrate sub-kingdom. The classes of Vertebrates make their appearance, on the whole, in the order indicated by their zoological position, the lowest first and the highest last. Where apparent exceptions occur, a reasonable explanation can be given, or our knowledge can be shown to be defective. Thus, the Fishes constitute the lowest group of Vertebrates, and in accordance with this they are the first to make their appearance (in the Silurian period). The Amphibians stand next to the Fishes in zoological rank, and they are the next group of Vertebrates to make their appearance, their earliest known representatives being found towards the close of the Palæozoic period (in the Carboniferous system). A little later than the *Amphibia* (in the Permian period) appear the Reptiles, which constitute the next highest class of Vertebrates. The class of Birds, the next in the series, possesses a palæontological record so fragmentary that we may leave it out of account in this connection ; but the last and highest group of Vertebrates, that of the Mammals, appears for the first time towards the close of the Triassic period. It need only be added, that the gene-

ral progression of zoological types, indicated by the successive introduction of the great classes of Vertebrates in the order of their zoological rank, is amply confirmed and strengthened by what is known as to the geological history of all the great groups of animals of which we have a fairly complete record. Even as regards the Invertebrate sub-kingdoms, where we are admittedly ignorant of the first appearance of the main divisions, we are nevertheless commonly able to show that the minor groups have been successively introduced in the order of their zoological rank. At the same time, it is to be borne in mind that zoological groups do not usually appear for the first time in either their lowest or highest forms. The earliest representatives of each group are, on the other hand, very usually "generalised" types, which have the capacity for either elevation or degeneration in their later development.

9. *The Absence of closely graduated transitional Forms between allied Morphological Types.*—While the general testimony of Palæontology is overwhelmingly in favour of the view that some general law of evolution has operated in the production of the varied forms of life which now exist or have existed in the past, there is no *direct* palæontological evidence which would certainly establish any particular theory as to the precise *modus operandi* of this law. With regard more particularly to the theory of "the origin of species by means of natural selection," which the world owes to the genius of Darwin, the evidence of Palæontology cannot be said to be conclusive. More especially, we have in most cases no sufficient evidence of the former existence of the numerous and closely graduated transitional forms between different species, which must, on this theory, have once existed. It is an essential part of the theory of natural selection that the production of any given species from any pre-existing species can only have been effected through the intervention of a long series of intermediate or transitional forms. It is true that many extinct animals are known which are clearly transitional between existing groups, now more or less widely separated from one another. It is also true that in a certain number of instances (particularly among the Molluscs) it has been found possible to connect two different specific types by means of a long series of intermediate links, the separate members of the series differing only in minute characters. As a general rule, however, the known transitional forms between allied groups are few in number, and are so far isolated from one another and from the forms they connect as to be in themselves absolutely distinct morphological types. It cannot be denied, therefore, that palæontology has, so far, to a large extent, failed to bring forward the numerous and *closely graduated* series of intermediate forms which must at one time have existed, supposing "natural selection" to be the sole agent in the origination of new species. The absence

of a sufficient number of such transitional forms, and the insufficient connection between such as are known to exist, may doubtless be in part explained by the known "imperfection of the geological record"; but this does not appear to offer an adequate solution of the difficulty. The theory of "the origin of species by means of natural selection," as elaborated by the master-mind of Darwin, constitutes, nevertheless, an invaluable, indeed an indispensable, guide in all branches of palæontological research.

LITERATURE.

[With regard to the subjects dealt with in the introductory portion of this work, the following are some of the original sources of information to which the student may have recourse. It is to be remembered, however, in the case of this, as of subsequent bibliographical lists of a similar character, that nothing more has been attempted than to give a selection of the more important original memoirs.]

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PART II.

PALÆOZOOLOGY

INVERTEBRATA

BY

H. ALLEYNE NICHOLSON

PART II.

CHAPTER VIII.

SUB-KINGDOM I.—PROTOZOA.

THE sub-kingdom *Protozoa*, as the name implies, includes the most lowly organised members of the animal kingdom, and may be defined as comprising *animals composed of undifferentiated protoplasm, or, at most, of protoplasm so far differentiated as to have developed an outer "wall" and a central "nucleus," the organism in the latter case becoming a "cell." In no case are definite "tissues" developed by the differentiation of a primitive cellular aggregate. There is no proper "body-cavity"; no nervous system; and either no alimentary apparatus, or one of a rudimentary nature.*

The *Protozoa* are small, commonly microscopic animals, for the most part aquatic in their habits. The contractile, jelly-like protoplasm, or "sarcode," of which the body is composed may be entirely naked, or may have the power of secreting hard structures, of horn, lime, or flint. The following table exhibits the chief groups of the *Protozoa*.

CLASS I. GREGARINIDÆ.—Protozoa in which the body has the form of a simple cell, without any mouth-aperture, and destitute of the power of emitting "pseudopodia." The Gregarines are for the most part internal parasites, and possess no hard structures.

CLASS II.—RHIZOPODA (SARCODINA).—Protozoa which are destitute of a mouth, and have the power of emitting extensile and contractile processes of protoplasm ("pseudopodia"). The sarcode may or may not have the power of secreting hard structures.

Order 1. *Monera.—Ex.* Protamœba.
Order 2. *Amœbea.—Ex.* Amœba.
Order 3. *Foraminifera.—Ex.* Globigerina.
Order 4. *Radiolaria.—Ex.* Haliomma.
Order 5. *Heliozoa.—Ex.* Actinophrys.

Class III.—Infusoria (Infusorian Animalcules).—Protozoa which are typically provided with a mouth and rudimentary digestive cavity, which do not possess the power of emitting pseudopodia, but which are furnished with vibratile cilia or with contractile filaments. They are mostly microscopic in size, and are mostly destitute of the power of secreting hard skeletal structures.

Regarded palæontologically, we may eliminate from the *Protozoa* the entire class of the *Gregarinidæ*, with the Rhizopodous orders of the *Monera*[1] and *Amœbea*, no trace of the past existence of which has yet been obtained, or, from their soft-bodied nature, is ever likely to be. For all practical purposes the same may be said of the large and universally distributed class of the Infusorian Animalcules.[2] Some of these, however, possess chitinous or membranous cases, which might possibly be preserved in a fossil state; and Ehrenberg has found in the flints of the Chalk certain microscopic bodies, which he regarded as being the protective carapaces of *Peridinium* and allied forms of Flagellate Infusoria. With this doubtful exception, however, no Infusorian animalcule has ever been detected in the fossil state, though the class has doubtless existed from the most remote antiquity. There remain, then, only the three Rhizopodous orders of the *Foraminifera*, *Radiolaria*, and *Heliozoa*, in all of which the soft protoplasmic body is generally strengthened by hard structures of horn, lime, or flint. The last mentioned of these orders comprises fresh-water organisms, in which a skeleton is absent or imperfectly developed, and no traces of fossil *Heliozoa* have hitherto been met with. On the other hand, the *Foraminifera* and *Radiolaria* usually have a well-developed skeleton, and are more or less extensively represented as fossils, so that they demand attention separately and in detail.

Foraminifera.

The *Foraminifera* may be defined as *Rhizopoda in which the body is protected by a shell or "test," which is composed of carbonate of lime, or which may consist of particles of sand cemented together by some animal cement, or may be simply horny (chitinous). The body-substance gives out long and thread-like processes (pseudopodia), which interlace with one another to form a network, and often coalesce at their bases to form a continuous layer of sarcode outside the shell. The pseudopodia* (fig. 18) *reach the exterior either by perforations in*

[1] The "coccoliths" are sometimes regarded as being referable to the *Monera;* but they will be considered here as belonging to the vegetable kingdom, and they will be briefly described in speaking of fossil *Algæ*.

[2] "Fossil Infusoria" are often spoken of as forming more or less extensive deposits in the earth's crust, but the organisms so named are really *Diatoms* and *Polycystina*.

the walls of the shell, or simply by the mouth of the latter, or by both these sets of apertures combined.

From a palæontological point of view the only part of a Foraminifer with which we have to deal is the shell or "test," and there are several points to notice in this connection. Firstly, as regards the actual composition of the shell, it is in the majority of cases calcareous, or composed of carbonate of lime, but it is rarely chitinous, and it is not uncommonly "arenaceous"—that is, composed of

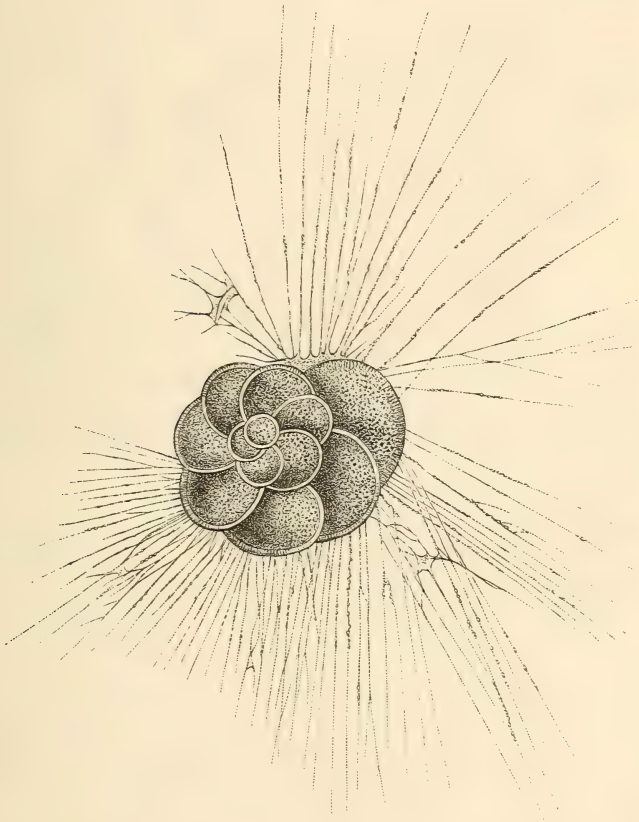


Fig. 18.—A many-chambered Foraminifer (*Rotalia veneta*) with the radiating and netted pseudopodia protruded. Greatly magnified. (After Max Schultze.)

particles of sand cemented together by some animal substance or by carbonate of lime. With the horny or chitinous *Foraminifera* (*Gromidæ*) we have nothing to do here, as they have never been, and are never likely to be, detected in a fossil condition.

An advance upon the chitinous shell is that presented by the so-called "arenaceous" *Foraminifera* (fig. 19), which are among the largest of the living types, the test being sometimes half an inch or more in length. In some cases the "arenaceous" test is nothing more than a chitinous envelope, protected by a layer of mud, or having sand-grains more or less largely embedded in its substance (H. B. Brady). Typically, however, the test of the arenaceous *Foraminifera* consists of sand-grains or other foreign particles united

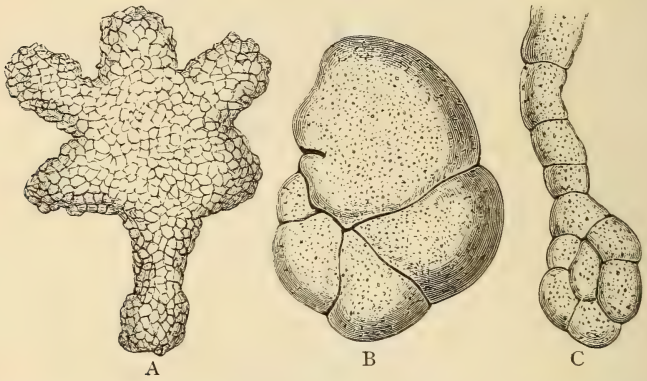


Fig. 19.—Shells of Arenaceous Foraminifera. A, Test of *Astrorhiza*, greatly enlarged; B, Test of *Trochammina ringens*, enlarged thirty times; C, Test of *Trochammina lituiformis*, enlarged eighteen times. (After W. B. Carpenter and Brady.)

together by a variable amount of cementing material, this latter containing from two to three per cent of carbonate of lime together with a notable proportion of peroxide of iron. The arenaceous *Foraminifera* have, as a rule, no pseudopodial apertures or "foramina" in the walls of the test, the pseudopodia being emitted from a single general or "oral" aperture, or from a number of apertures in the wall of the last chamber. Though normally "imperforate," there are, however, certain forms of the arenaceous or sub-arenaceous *Foraminifera* (such as *Valvulina*, *Nodosinella*, and *Endothyra*) in which the walls are pierced by pseudopodial foramina. Indeed, some degree of porosity appears to be commonly present, and in some forms there is no "oral aperture" to the test at all.

The great majority of the *Foraminifera* possess a shell composed essentially of carbonate of lime, with or without variable quantities of other constituents. Two chief varieties of these calcareous tests are known, termed respectively the "porcellanous" and the "hyaline" or "vitreous" types. In the so-called "porcellanous" types, the test is quite homogeneous in its composition, opaque-white when seen by reflected light, and destitute of pores or foramina

for the emission of pseudopodial filaments. In all the porcellanous *Foraminifera*, therefore, the shell is "*imperforate*," and the pseudopodia are emitted from a general "oral aperture." There is also reason to believe that the shell in these types is largely composed of aragonite. Though normally calcareous, the test may be encrusted by sand-grains, or it may be composed of siliceous particles embedded in a chitinous envelope, or, as shown by Dr H. B. Brady to sometimes occur in examples of *Miliola* dredged from great depths, it may even be genuinely siliceous. On the other hand, in the so-called "hyaline" or "vitreous" types of the *Foraminifera*, the calcareous test (composed principally of calcite) is glassy and transparent, and its walls are perforated by numerous minute tubes through which the pseudopodia are emitted. In the series of the hyaline *Foraminifera*, therefore, the test is said to be "*perforate*." Hence, in vertical sections of the shell of any such type (*e.g.*, *Globigerina*), the test is seen under the microscope to be traversed by closely set tubules, running at right angles to the outer and inner

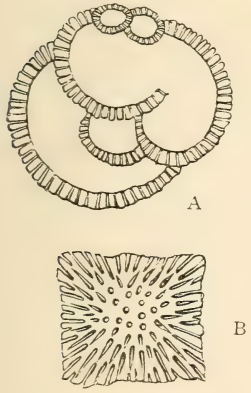


Fig. 20.—A, Vertical section of the test of *Globigerina bulloides*, highly magnified, showing the pseudopodial tubes; B, Tangential section of the same, showing the tubules in transverse section. (Original.)

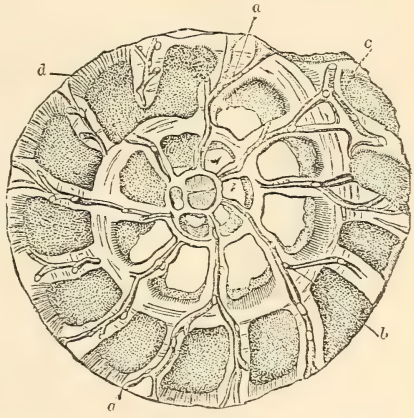


Fig. 21.—Section of the shell of *Rotalia Schræteriana*, magnified, showing pseudopodial tubes in the walls (*d*). The test is also traversed by a series of radiating and transverse canals (*a*, *b*, *c*). (After Williamson and Carpenter.)

surfaces of the shell; while in tangential sections (*i.e.*, sections parallel with the surface) these tubules are transversely divided, and appear as dark spots or clear pores (see figs. 20 and 21).

The presence, or absence, of pseudopodial tubes in the walls of the test has been employed as a character whereby the entire group of the *Foraminifera* might be divided into the two sections of the *Perforata* and *Imperforata*; the former including the hyaline or

vitreous types, while in the latter are comprised the "porcellanous," "arenaceous," and "chitinous" types. It has been shown, however, that this division is not strictly natural, since various arenaceous types possess a test which is more or less extensively porous. It would appear, in fact, that the composition of the shell is liable to variation, in accordance with the nature of the material obtainable by the organism at any particular station, and that it is therefore possible to attach too great value to this character in framing a classification of the *Foraminifera*.

Again, as regards the *form* of the shell, great differences exist among the *Foraminifera*, and as concerns the mere external configuration, this is so variable that little or no value can be attached to it in classification. Moreover, in the two great series of the Perforate and the Imperforate *Foraminifera* it is common to find parallel or "isomorphic" groups. That is to say, we meet with two series of forms, repeating each other's peculiarities and variations in *form*, but the shell in the one series being perforate, while in the other it is imperforate.

The simplest form among the *Foraminifera* is that of a single spheroid of sarcode, capable of secreting for itself a hard covering, as in the flask-shaped *Lagena* (fig. 29, *f*) or the globular *Orbulina* (fig. 22). Forms such as these are said to be "unilocular" or "monothalamous," the test consisting of but a single chamber, not subdivided by partitions or "septa." In the more complex *Foraminifera*, the sarcode of the body undergoes a subdivision into partially separated segments, produced by constrictions in the growing protoplasm, and each of these segments becomes more or less completely divided off from its neighbours, or enclosed by a wall of shell. In these "multilocular" or "polythalamous" *Foraminifera*, therefore, the shell ultimately comes to consist of a series of chambers, separated by partitions of the test, and filled with sarcode. The partitions, or "septa," between the different chambers, are, however, perforated by one or more apertures, through which pass connecting bands, or "stolons," of sarcode; so that the sarcode occupying the different chambers is united into a continuous and organic whole. Each segment may give out its own pseudopodia through perforations in its investing wall (fig. 18), or the pseudopodia may be simply emitted from the mouth of the shell by the last segment only. In any case, the direction in which the segments are developed is governed by a determinate law, and differs in different species, the form ultimately assumed by the shell depending wholly upon this. The forms assumed by the shells of *Foraminifera* are,

Fig. 22.—*Orbulina universa*. A simple Foraminifer from the Pliocene strata (Sub-Apennine beds) of Italy. (D'Orbigny).

however, extremely variable, even within the limits of a single species, and it would be impossible to notice even the chief types in this place. There are, however, two or three important variations which may be mentioned. If the buds are thrown out from the primitive spherule in a linear series so as to form a shell composed of numerous chambers arranged in a straight line, we get such a type as *Nodosaria* (fig. 29, *g*). When the new chambers are added in a spiral direction, each being a little larger than the one which preceded it, and the coils of the spiral lying in the same plane, we get such a form as *Cristellaria* (fig. 23). These are the so-called "nautiloid" *Foraminifera*, named from the resemblance of the shell, in figure, to that of the Pearly Nautilus. From this resemblance the nautiloid *Foraminifera* were originally placed in the same class as the *Ammonites* (*Cephalopoda*), but their true position was shown by the examination of their soft parts. In the typical nautiloid shell the convolutions of the spiral all lie in one plane; but in other cases, as in *Rotalia* or *Pulvinulina* (fig. 24), the shell becomes turreted or top-shaped, in consequence of the coils of the spiral passing obliquely round a

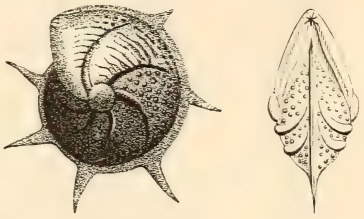


Fig. 23.—*Cristellaria echinata*, a "nautiloid" Foraminifer. (D'Orbigny.)

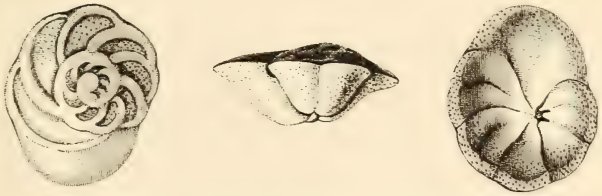


Fig. 24.—*Pulvinulina Boueana*. (D'Orbigny.)

central axis. In other cases, as in *Tinoporus*, the chambers are arranged in an irregular or "acervuline" manner.

In the majority of the polythalamous *Foraminifera*, the successive chambers of the test are so produced that the septum between any two of them is formed solely by the anterior wall of the older chamber, which thus constitutes the posterior wall of the newer one (fig. 25). In the highest types of the compound *Foraminifera*, however, each chamber is provided with its own proper wall of shell, each segment, as it is produced, forming for itself a posterior wall which applies itself to the anterior wall of the preceding segment; so that each septum ("septal plane") is composed of *two* lamellæ, as seen

in fig. 26, A (Carpenter). Moreover, "in the higher types of the hyaline or vitreous series we frequently meet with an 'intermediate' or 'supplemental' skeleton, formed by a secondary or exogenous deposit upon the outer walls of the chambers, by which they receive a great accession of strength. This deposit not only fills up what would otherwise be superficial hollows at the junctions of the chambers (fig. 26, A *d*), or (as in *Polystomella*) at the umbilical depression, but often forms a layer of considerable thickness over the whole surface, thus separating each whorl from that which encloses it; and it is sometimes prolonged into outgrowths that give a very peculiar variety to the ordinary contour, as in some varieties of *Rotalia* and *Polystomella*, but most characteristically in *Calcarina* (fig. 26, B), and the stellate form of *Tinoporus*. This intermediate or supplemental skeleton, wherever developed to any considerable extent, is traversed by a set of 'canals,' which are usually arranged upon a systematic plan, and are sometimes distributed with considerable minuteness" (Carpenter). The canals of this system are doubtless filled in the living state by prolongations of the sarcode, which serve to keep up the vitality of the intermediate skeleton. This intermediate skeleton, with its canal-system, is largely developed in many of the highest and largest of the types of the hyaline *Foraminifera*, and very specially so in the "Nummulites" and their immediate allies.

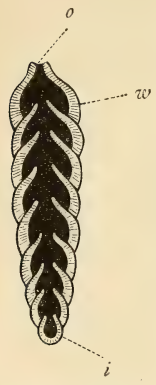


Fig. 25.—Section of the shell of *Nodosaria rapa*, showing the mode of formation of the successive chambers. *o* Oral aperture of the test; *w* Wall; *i* Primordial chamber.

As regards the distribution of the *Foraminifera* in *space*, a few forms (all belonging to the single family of the *Gromidæ*) are freshwater in habit, but the vast majority are inhabitants of the sea.

As regards the marine forms, very many species live in comparatively shallow water, but certain forms are found at great depths in the ocean. A small number of forms, belonging, according to Dr Henry B. Brady, to eight or nine genera, are pelagic in their habits, and "pass their existence, either in part or entirely, at the surface of the ocean or in mid-water." Though only a few genera have pelagic representatives, these few are of great importance, owing to the extraordinary profusion in which they occur individually. The principal pelagic genus is *Globigerina*, most of the species of which live in the open sea, though one species of the genus seems to always live at the bottom. The shells of the pelagic *Foraminifera*, after the death of the animal, fall to the bottom of the sea, where they accumulate to form (along with the shells of the species which live habitually at the bottom) great deposits of "Foraminiferal mud."

The most important deposit of this nature at the present day is the well-known "Globigerina ooze," which is found to cover vast areas of the sea-bottom in all the great oceans, mostly at depths of from 600 to about 2500 fathoms, and which is of special interest from the resemblances which it presents to the White Chalk. The "Globigerina ooze" is a whitish or greyish mud, principally composed of carbonate of lime, but containing a considerable proportion of silice-

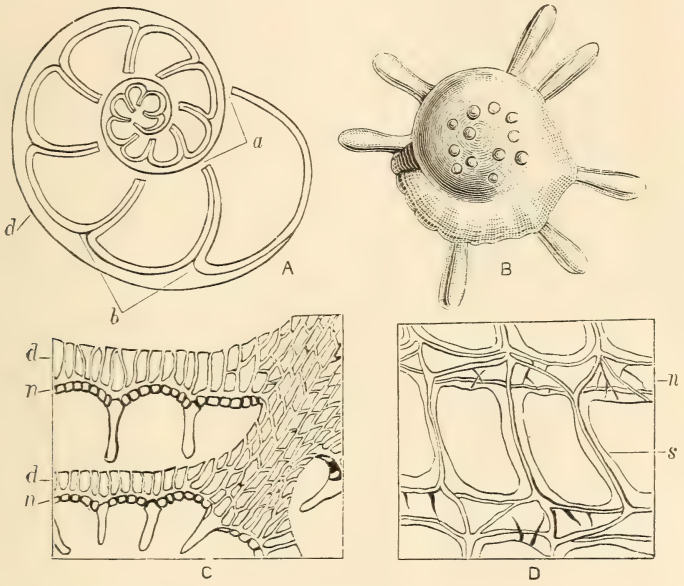


Fig. 26.—A, Diagram of one of the higher forms of the vitreous *Foraminifera*, showing the double nature of the septa (*b*), the stolon-passages between successive chambers (*a*), and the supplemental skeleton (*d*); B, Test of *Calcarina Spengleri*, magnified twelve diameters, showing the spines formed by the supplemental skeleton; C, Part of a section of the test of *Calcarina*, magnified fifty diameters, showing the tubulated "proper walls" of the chambers (*n*), and the canal-system of the intermediate skeleton (*d*); D, Part of the test of *Nummulina lævigata*, highly magnified, showing the canal-system of the septa (*s*), and marginal cord (*n*). (After Carpenter.)

ous matter, along with a variable quantity of subordinate ingredients such as alumina. When examined microscopically, the Globigerina mud (fig. 27) is found to consist principally of the entire or broken shells of *Foraminifera*, belonging mostly to the genera *Globigerina*, *Orbulina*, *Hastigerina*, and *Pulvinulina*, together with many of the singular calcareous organisms known as "coccoliths." In the nature of the organisms of which it is composed, the Globigerina ooze of the present day presents the closest resemblance to White Chalk; while the chemical differences between them—especially as regards the relative percentage of silica—admit, as will be more particularly

pointed out hereafter, of satisfactory explanation. There are, however, other differences between the two, especially as regards the characters of the Molluscan fauna of the latter, which would indicate that the Globigerina ooze and the White Chalk were not formed under conditions precisely alike.

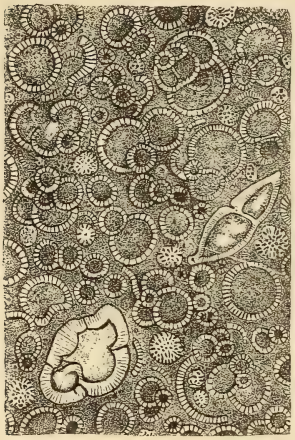


Fig. 27.—Section of hardened Globigerina ooze, enlarged about twelve times. Recent. (Original.)

As regards the distribution of the *Foraminifera* in *time*, representatives of the group are found in almost all, or in all, rock-groups in which limestones are developed from the Ordovician period onward. Leaving the much disputed *Eozoön* on one side, no remains of *Foraminifera* have hitherto been recognised as occurring in any deposit older than the Ordovician. As regards the older rocks, the remains of *Foraminifera* are usually found most abundantly in limestones, or in calcareous shales, and particularly in the shaly partings which separate calcareous bands. In many cases, they have contributed notably to the composition of the solid crust of the earth, and have often built up massive and widely extended limestones. In other cases, where they are present in smaller quantity, they may be commonly detected in thin sections of limestone. In some instances, the tests of *Foraminifera* have been infiltrated, prior to fossilisation, with glauconite (silicate of iron and potash), and the actual shell has subsequently been dissolved away. In some of the warmer seas of the present day, green sands are found to be in course of deposition, the grains of which are largely composed of internal casts in glauconite of the shells of *Foraminifera ;* and it is probable that the green grains of various deposits, and especially of the Cretaceous system, are in part of a similar nature.

If we omit the group of the *Receptaculitidæ*, regarded by Hinde as referable to the *Porifera*, the Ordovician, Silurian, and Devonian limestones exhibit in general a remarkable, and, in fact, an unaccountable, absence of the remains of *Foraminifera ;* since the variety of the types of these organisms represented in the limestones of the Carboniferous period would justify the conclusion that the order is one of very high antiquity. The remains of *Foraminifera* are not, however, absolutely wanting in these ancient deposits, since the recent genus *Saccammina* has been found to occur in rocks of Ordovician age, while the Devonian limestones occasionally con-

tain the tests of *Foraminifera*. In the Carboniferous period, most of the limestones can be shown by microscopical examination to contain the shells of *Foraminifera* in larger or smaller numbers (see fig. 4); and some of them are so largely composed of the cases of these minute organisms as to become truly "Foraminiferal limestones." Of this nature are the great Fusulina limestones of Russia and North America, and the Saccammina limestone of Britain. It is interesting to notice that the highly specialised genus *Nummulina*, which attained such a vast development in the Tertiary period, is represented for the first time in the Carboniferous limestone. In the Permian limestones *Foraminifera* are tolerably abundant, but on the whole nearly resemble their Carboniferous predecessors.

In the Mesozoic period, the remains of *Foraminifera* are more or less abundant in the Triassic and Jurassic systems, occurring in limestones, shales, or marls, and sometimes being present in sufficient numbers to give rise to regular Foraminiferal limestones. In the Cretaceous period, the most remarkable Foraminiferal rock is the White Chalk itself. This well-known and widely extended formation can be readily shown by microscopical investigation to be very largely made up of the entire or broken shells of *Foraminifera*, amongst which the genus *Globigerina* plays a predominant part (fig. 28). There is thus a close and striking similarity between the White Chalk and the "Globigerina ooze" of modern seas. The principal distinction between Chalk and consolidated Globigerina mud is found in the fact that the latter contains a considerable proportion of siliceous matter, while the former consists of from ninety-five to ninety-eight per cent of carbonate of lime, and is nearly or quite free from disseminated silica. This distinction is, however, more apparent than real, and depends in reality upon the changes which the Chalk has undergone subsequent to its original deposition. The siliceous matter in the modern Globigerina mud is due to the presence of a larger or smaller intermixture of the flinty tests of Radiolarians, the spicules of siliceous Sponges, the tests of Diatoms, and the like. There is no reason to doubt, however, that the Chalk, when first laid down, similarly contained a larger or smaller quantity of siliceous matter in the form of the skeletons of flint-producing organisms such as Sponges. The silica of these

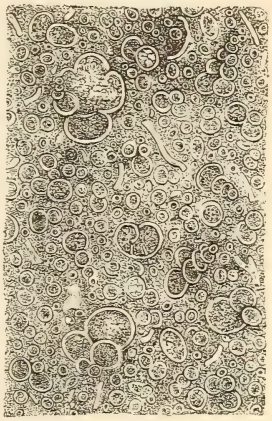


Fig. 28. — Section of White Chalk, from Sussex, enlarged about fifty times. (Original.)

skeletons in course of time underwent solution, and the siliceous Sponges are now found in the White Chalk only in the form of casts, or with their original skeleton replaced by some such substance as peroxide of iron. The dissolved silica thus produced was ultimately segregated from the mass of the Chalk, and is now represented by the nodules of flint which form such a characteristic feature of parts of the White Chalk. It would appear, therefore, that the White Chalk in its original chemical composition must have been very closely similar to the modern Globigerina ooze; and it is a reasonable conclusion from its general purity that it must, like its modern analogue, have been deposited in a deep and open ocean, at a considerable distance from land. At the same time, the characters of the *Mollusca* which are predominant in the Chalk, would go to show that this remarkable Foraminiferal deposit must have been laid down in general at depths less than those at which the modern Globigerina ooze is now accumulated.

In the Tertiary period, lastly, the remains of *Foraminifera* are abundant and varied, and are often present in such numbers as to give rise to more or less extensive Foraminiferal limestones. The most notable of these is the great "Nummulitic limestone" of the Eocene. In the later Tertiary deposits, the genera represented are mostly those now in existence, and many of the species are identical with living forms. The *Foraminifera*, in fact, like other lowly organised forms, have been very "persistent" types of life. A number of the Cretaceous species, indeed, appear to be inseparable from existing forms, while some living species are believed to date from even an earlier period. As regards the *genera*, the prevalent types in Carboniferous times still survive unchanged; and Dr Carpenter has enunciated the conclusion that upon the whole "there is no evidence of any fundamental modification or advance of the Foraminiferous type from the Palæozoic period to the present time."

Classification of the Foraminifera. — The classification of the *Foraminifera* has proved a matter of considerable difficulty. The older arrangements were unnatural, as being based wholly on the form of the shell, a point in which the *Foraminifera* show a most marvellous variability. For this reason, the artificial systems proposed by D'Orbigny and Max Schultze have now been generally abandoned, and their place has been taken by other more natural schemes of classification, and especially by those put forward independently and almost simultaneously by Professor von Reuss upon the Continent, and by Dr W. B. Carpenter, Mr Parker, and Professor T. Rupert Jones in this country. Both these arrangements agree in the essential feature that they divide the *Foraminifera* into two great primary divisions, in accordance with the nature of the shelly investment. In the one division (*Imperforata*), the test is not perforated

by pseudopodial apertures, and it may be either "arenaceous" or "porcellanous." In the other division, the test is perforated by more or less numerous pseudopodial foramina, and to this division the name of *Perforata* is applied. The following tables exhibit the arrangements proposed by Carpenter, Parker, and Rupert Jones, on the one hand, and Reuss, on the other hand: the former being the most natural, and the one most widely adopted:—

A. Classification of the Foraminifera, according to Carpenter, Parker, and Rupert Jones.

Sub-Order I. Imperforata.—Test membranous, calcareous, or arenaceous, not perforated by pseudopodial foramina.

Family 1. *Gromida.* Family 2. *Miliolida.*
Family 3. *Lituolida.*

Sub-Order II. Perforata.—Test perforated by pseudopodial foramina, generally calcareous.

Family 1. *Lagenida.* Family 2. *Globigerinida.*
Family 3. *Nummulinida.*

B. Classification of the Foraminifera according to Reuss.

I. Foraminifera with a Non-perforate Test.

A.—With arenaceous tests.

1. *Lituolidea.* 2. *Uvellidea.*

B.—With compact, porcellanous, calcareous tests.

1. *Squamulinidea.* 3. *Peneroplidea.*
2. *Miliolidea.* 4. *Orbitulitidea.*

II. Foraminifera with a Perforate Test.

A.—With a glassy, finely porous, calcareous test.

1. *Spirillinidea.* 5. *Polymorphinidea.*
2. *Ovulitidea.* 6. *Cryptostegia.*
3. *Rhabdoidea.* 7. *Textilaridea.*
4. *Cristellaridea.* 8. *Cassidulinidea.*

B.—With an exceedingly porous, calcareous test.

1. *Rotalidea.*

C.—With a calcareous shell, traversed by a ramified canal-system.

1. *Polystomellidea.* 2. *Nummulitidea.*

On the other hand, Dr H. B. Brady, one of the highest living authorities on the *Foraminifera*, has recently pointed out that, in the light of our present knowledge, the primary division of the order into the two sections of the *Perforata* and *Imperforata* cannot be

considered to be natural. It is now well known that many of the Arenaceous *Foraminifera*, forming one of the principal groups in the old section of the *Imperforata*, have diffused pseudopodial apertures, with or without a general aperture as well, so that their test is truly "perforate." The retention of the sections *Perforata* and *Imperforata* would therefore necessitate the splitting up of the Arenaceous *Foraminifera* into two series, one with a "perforate" and the other with an "imperforate" test. In view of this fact, Dr Brady has abandoned the minute structure of the test as an exclusive basis for the classification of the *Foraminifera*, and has proposed the following arrangement of the order into families :—

ORDER FORAMINIFERA (RETICULARIA).

Family 1. GROMIDÆ.—Test chitinous; smooth or encrusted with foreign bodies; with a pseudopodial aperture at one or both extremities. *Ex.—Gromia, Microgromia, Lieberkühnia.*

Family 2. MILIOLIDÆ.—Test imperforate; normally calcareous and porcellanous, sometimes encrusted with sand, or, under certain conditions, chitinous or siliceous. *Ex.—Biloculina, Peneroplis, Orbitolites.*

Family 3. ASTRORHIZIDÆ.—Test composed of sand-grains or other foreign bodies, usually more or less united into a coherent test by a cementing material. Usually the test is monothalamous, often branched or radiate, sometimes partially subdivided, but seldom or never truly septate. *Ex.—Astrorhiza* (fig. 19, A), *Rhabdammina, Saccammina.*

Family 4. LITUOLIDÆ.—Test arenaceous, usually regular in contour; septation of the polythalamous forms often imperfect; chambers frequently labyrinthic. *Ex.—Lituola, Trochammina* (fig. 19, B and C), *Endothyra.*

Family 5. TEXTULARIDÆ.—Tests of the larger species arenaceous, with or without a perforate calcareous basis; smaller forms hyaline and perforated. Chambers arranged in two or more alternating series, or spiral, or confused. *Ex.—Textularia, Valvulina.*

Family 6. CHILOSTOMELLIDÆ.—Test calcareous, perforate, polythalamous. Segments following each other from the same end of the long axis, or alternately at the two ends, or in cycles of three; more or less embracing. Aperture a curved slit at the end or margin of the final segment. *Ex.—Chilostomella.*

Family 7. LAGENIDÆ.—Test calcareous, finely perforated; either monothalamous, or consisting of a number of chambers joined in a straight, curved, spiral, alternating, or (rarely) branched series. Aperture simple or radiate, terminal. No interseptal skeleton nor canal-system. *Ex.—Lagena, Nodosaria, Cristellaria.*

Family 8. GLOBIGERINIDÆ.—Test free, calcareous, perforate; chambers few, inflated, arranged spirally. Aperture single or multiple, conspicuous. No supplementary skeleton nor canal-system. *Ex.—Globigerina, Orbulina.*

Family 9. ROTALIDÆ.—Test calcareous, perforate; free or adherent. Typically spiral and "rotaliform"—*i.e.*, coiled in such a manner that the whole of the segments are visible on the upper surface, those of the last convolution only on the inferior or apertural side, sometimes one face being more convex, sometimes the other. Aberrant forms evolute, outspread, acervuline or irregular. Some of the higher modifications with

double chamber-walls, supplemental skeleton, and a system of canals. *Ex.—Rotalia, Discorbina, Carpenteria, Calcarina, Tinoporus.*

Family 10. NUMMULINIDÆ.—Test calcareous and finely tubulated; typically free, polythalamous, and symmetrically spiral. Usually a "supplemental skeleton" and canal-system. *Ex.—Nummulina, Polystomella, Fusulina, Nonionina.*

In connection with the general subject of the classification of the *Foraminifera*, the following remarks by Dr Brady may advantageously be quoted; since they not only have a most important bearing upon the special point in question, but forcibly express the principles which should guide the philosophic naturalist in his systematic treatment of all such variable forms of life: "A purely artificial classification is ill adapted to the conditions presented by a class of organisms like the *Foraminifera*, largely made up of groups of which the modifications run in parallel lines. This 'isomorphism,' demonstrated chiefly by the labours of Messrs Parker and Jones, whilst it is the source of most of the difficulties the systematist has to contend with, is, at the same time, the key to the natural history of the order as at present accepted. It exists not merely between a single series, in one of the larger divisions, with a single series in another, but often amongst several series even of the same family. It not unfrequently happens that a member of one group presents a greater similarity to its isomorph in another group, with which it has no relationship, than it does to any other member of its own group. Take a familiar illustration—suppose the fingers of the two hands to represent the modifications ('species') of two such parallel types of *Foraminifera*: the thumb of one hand resembles more closely the thumb of the other hand than it does any other of the fingers on its own. In other words, the extreme member of one series bears greater similarity to its isomorph in the other series than it does to its own nearer relations, and so on through the remaining members of the respective groups. Under conditions like these, artificial subdivision, based upon minor morphological characters, is certain to infringe the order of nature, owing to its tendency in some cases to separate forms closely allied, and in others to place together such as have no natural affinity."

The principal fossil groups of *Foraminifera* require a brief consideration, but in the short summary of these which follows—as in the case of similar summaries which will subsequently be given—it will be understood that nothing further is proposed than to select for notice and characterisation those *leading types* of each great group of fossils which may seem to demand mention on the ground of their being common, or in other respects, geologically or zoologically, of peculiar importance. For anything like a complete list of the known structural types of each group, or the characters of all the recorded

genera, the specialist will consult special treatises; and it does not appear to be necessary for the wants of ordinary students to do more than to supply a brief statement of the conspicuous characters—especially the *differential* characters—of the more widely distributed and more important types in each group. Nor can even this limited characterisation of leading types be carried out with equal fulness in the case of all groups of fossils, or upon any absolutely uniform plan. In the case, however, of Invertebrate fossils, as being those with which the palæontologist is more especially called upon to deal, the families of each group will, where possible, be defined, and some of the chief generic types will be noticed. The subjoined engraving, representing some of the principal type-forms of the *Foraminifera*, is from a drawing kindly made for the author by his friend, Dr Henry Brady, who has so greatly contributed to our knowledge of this difficult group of organisms.

The first family of the old division of the Imperforate *Foraminifera*, that of the *Gromidæ*, requires no special consideration from a palæontological point of view, as it is not represented by any fossil forms. Most of the *Gromidæ* are inhabitants of fresh waters, and they possess a thin, chitinous, imperforate shell, sometimes encrusted with foreign bodies, and with a general pseudopodial aperture at one or both ends. Owing to the horny character of the shell, it is hardly probable that any members of this family will ever be discovered in the fossil condition.

In the family of the *Miliolidæ*, the test is opaque, porcellanous, unilocular, or multilocular, and extremely variable in shape; the oral aperture being simple and undivided, or being formed by numerous pores. The family, as far as known at present, is not represented in the Palæozoic period, but ranges from the Trias to the Recent period inclusive. One of the simplest forms of this group is *Cornuspira* (fig. 29, *a*), in which the shell is a simple unchambered spiral, like the shell of a *Planorbis*. The genus is represented for the first time in the Lias, and is found under living forms in our seas. *Nubecularia* is a still older type, beginning in the Trias, and its test, extraordinarily variable in shape, is usually parasitic upon shells and other foreign bodies. In *Miliola*, again (fig. 29, *b*, representing the sub-generic form *Quinqueloculina*), the shell is still extremely variable in form, but it consists typically (*Biloculina*) of a series of chambers wound round an axis, in such a manner that each embraces half the entire circumference. This genus dates from the Trias, and is well represented in recent seas. It abounded in Eocene times, one of the Tertiary limestones of the Paris basin being known as the "Miliolite limestone," in consequence of its being largely made up of the shells of a *Miliola*. In *Peneroplis* (fig. 29, *c*), which is closely allied to *Cornuspira*, the shell is a flattened spiral, which

expands very rapidly in its last half turn, the mouth running along the length of the base, and being constituted by numerous isolated

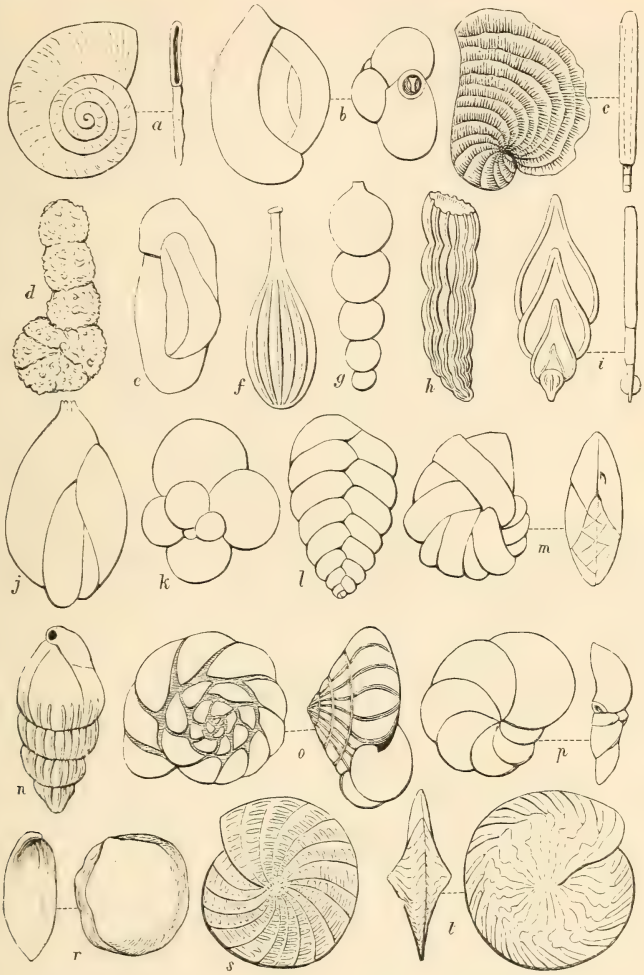


Fig. 29.—Types of Foraminifera. *a, Cornuspira foliacea; b, Quinqueloculina seminulum; c, Peneroplis pertusus; d, Lituola agglutinans; e, Trochammina pusilla; f, Lagena sulcata; g, Nodosaria radicula; h, Marginulina raphanus; i, Frondicularia Archiaciana; j, Polymorphina lactea; k, Globigerina bulloides; l, Textularia sagittula; m, Cassidulina lævigata; n, Bulimina Buchiana; o, Rotalia Beccarii; p, Truncatulina lobatula; r, Archæodiscus Karreri; s, Polystomella crispa; t, Amphistegina Lessoni.* All the figures are greatly enlarged, the real diameters varying from 1-100 to 1-10 inch. (H. B. Brady.)

pores. It ranges from the Eocene to the present day. Much more complicated types of the *Miliolidæ* are *Alveolina* and *Orbitolites.*

The former has a comparatively large fusiform shell, consisting of many layers of chambers rolled up spirally round an elongated axis, the last series opening by a row of pores. It dates from the Cretaceous period, and has largely contributed to the formation of various of the Tertiary limestones. The latter is coin-shaped, sometimes more than half an inch in diameter, and very complex as regards the arrangement of its chambers. The genus is especially abundant in the Eocene Tertiary, but it dates from the Lias, and occurs plentifully in recent seas.

The next family of the *Foraminifera* is that of the *Astrorhizidæ*, comprising a number of interesting types, sometimes of considerable size, in which the test is composed of sand-grains or other foreign particles, generally united by a cementing basis, but sometimes slightly or not at all consolidated. The test may be monothalamous or polythalamous, but in the latter case genuine internal septa do not exist. The shell is often branched or radiate, and may attain a considerable size. The type-genus of this family is *Astrorhiza* itself (fig. 19, A), which is not known to occur in the fossil condition, its test, though of considerable thickness, having its component grains very imperfectly cemented together. A much firmer and more compact shell is possessed by the genus *Saccammina*, which merits special mention as being the only Foraminifer which in Britain can be said to actually form a limestone. It consists of free spherical, pyriform, or fusiform chambers (fig. 30), sometimes separate, sometimes united end to end in twos or threes, with thick, internally labyrinthic walls. The central chamber communicates with the exterior by a single aperture, and the average length of the chambers of the British Carboniferous species (*Saccammina Carteri*, Brady) is as much as 1-8th inch. It forms beds of limestone in the Carboniferous of the South of Scotland and North of England; but the genus is not known to occur again till we meet it in the Post-Pliocene, and, in a living state, in the North Sea. The genus is, however, of a much higher antiquity than the Carboniferous, since it is found to be largely represented in the Ordovician limestones of Ayrshire.

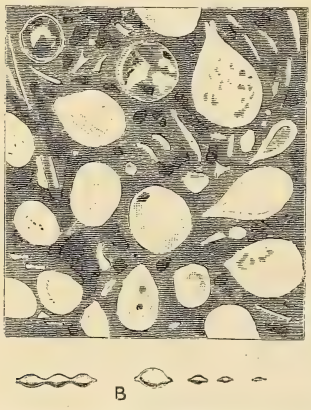


Fig. 30.—A, A slice of limestone with *Saccammina Carteri*, enlarged five diameters, from the Carboniferous Limestone of Elfhills, Northumberland. (After H. B. Brady.) B, Spheres of the same, of the natural size, exhibiting variations.

In a number of very interesting forms of the *Astrorhizidæ*, the test

is tubular, composed of arenaceous tubes, of which the sand-grains may be loosely or firmly cemented together, and which may be free or may be adherent along one side to foreign bodies. The tubular test may be branched or radiate, or may simply be more or less loosely coiled and contorted. One of the most remarkable recent types of this group is *Syringammina*, in which the test is described by Dr Brady as forming masses of branching, radiating tubes, arranged in more or less distinct layers or tiers. In *Hyperammina*, again, the test (fig. 31) has the form of a sandy tube, often of indefinite length,

Fig. 31.—The winding tubular test of *Hyperammina vagans*, adherent on one side to a piece of broken shell. *a* Initial chamber; *b* General pseudopodial aperture. The figure is enlarged fifteen diameters. Recent. (After H. B. Brady.)

with the closed end commonly inflated so as to form a distinct chamber, the pseudopodia being emitted from a general aperture at the opposite end of the tube. The tube in this genus may be free, or may be adherent to foreign bodies.

The forms just mentioned throw light upon some very remarkable fossils which occur in great numbers in certain of the Ordovician limestones of Britain and North America, and which have been described under the generic name of *Girvanella* (= *Strephochetus*). The fossils in question present themselves in the form of small rounded or irregular nodules (fig. 32, A), which are sometimes so abundant as to constitute a conspicuous element in the limestone. When broken, these nodules show a distinctly concentric structure, and when examined by means of thin sections (fig. 32, B), they are found to consist of exceedingly minute circular tubes (about 1-45 millimetre in diameter), endlessly contorted and bent, and twisted

together in loosely reticulate or vermiculate aggregations. The most probable view of the relationships of this singular fossil is that it is an

Fig. 32.—A, Fragment of limestone from the Ordovician rocks of Craighead, Girvan, of the natural size, showing numerous exceptionally large masses of *Girvanella problematica*; B, Section of a minute mass of *Girvanella*, enlarged about sixty times. (Original.)

Arenaceous Foraminifer, allied to the recent genera *Syringammina* and *Hyperammina*.

The last group of the so-called "Imperforate" *Foraminifera* is that of the *Lituolidæ*, comprising an extensive series of arenaceous types, in which the shell consists essentially of particles of coarse or fine sand cemented together more or less firmly. In many cases the cement is calcareous, and though the shell is usually imperforate, the walls are in other cases pierced by pseudopodial apertures. Sometimes the test consists of purely calcareous particles embedded in a calcareous cement. In *Lituola* itself, the type of the group (fig. 29, *d*), the test is generally crosier-shaped, sometimes nautiloid, usually with a rough exterior, and composed of sand-grains agglutinated together. The genus ranges from the Carboniferous to the present day. An essentially Carboniferous type is *Endothyra*, in which the shell is nautiloid, or resembles that of a *Rotalia* in shape, and is found abundantly in the Mountain Limestone of Britain. It forms in America entire beds of the Carboniferous Limestone (fig. 33). Allied to *Endothyra* is the Liassic

Fig. 33.—Section of Carboniferous Limestone from Spergen Hill, Indiana, U.S., showing numerous large-sized *Foraminifera* (*Endothyra*) and a few oolitic grains magnified. (Original.)

genus *Involutina*, formerly placed among the Rotaline Foraminifera. In *Trochammina* (fig. 29, *e*) the test is usually spiral, consisting of one or many chambers, free or attached, and, though sandy, with a smooth surface. It ranges from the Carboniferous to the present day. *Valvulina* (fig. 34) also generally has a spiral shell which may be free or attached, and is normally thick-walled, imperforate, and sandy. Sometimes, however, the shell is porous and smooth, and in other cases the sandy coating seems to be a mere encrustation on a calcareous and perforate shell, so that *Valvulina* (which is by Brady included in the family of the *Textularidæ*) may be regarded as a transitional type between the series of the imperforate and perforate *Foraminifera*. The genus makes its first appearance in the Carboniferous of Britain, is abundant in the Tertiaries, and is represented in existing seas. In the *Nodosinella* of the Carboniferous we have another curious type, closely resembling the well-known *Nodosaria* in *form*, but having a sub-arenaceous, imperforate test. A still more singular form is the *Stacheia* of the Carboniferous, in which the test is also sub-arenaceous and imperforate, but grows parasitically upon foreign bodies, in the shape of a crust composed of "an acervuline mass of chamberlets" (Brady). Lastly, there is a peculiar group of the *Lituolidæ* represented by the recent *Cyclammina* and the extinct *Loftusia*, in which the test is sandy, and the finely arenaceous shell-wall is irregularly cancellated, so as greatly to restrict the actual cavities of the chambers. In *Cyclammina* the shell is spiral and nautiloid, with numerous chambers arranged in an involute series. In the singular genus *Loftusia* (fig. 35), from the Eocene Tertiary of Persia, the test is fusiform, and may attain a length of from two to three inches. As regards its internal structure, the shell is composed of a spirally rolled lamella, the volutions of which run in the long axis of the test, and which is of a sandy texture and is much cancellated (fig. 35, B). The spaces between the volutions of the primary lamella are intersected by obliquely directed partitions, which are also cancellated in structure, and are connected by numerous irregular vertical pillars.

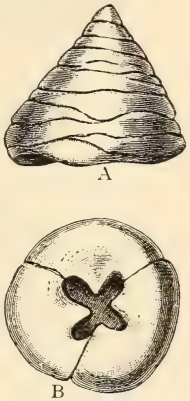
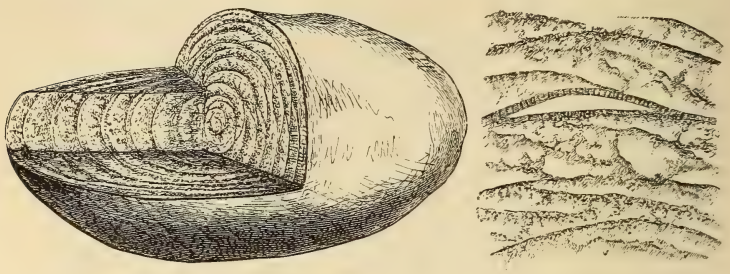


Fig. 34.—A, *Valvulina palæotrochus*, viewed in profile, and enlarged 45 diameters; B, The same viewed from below. Carboniferous Limestone. (After Brady.)

The genus *Parkeria*, which has commonly been referred here, has been shown by recent investigations to be truly referable to the *Hydrozoa*, and to be related to the existing *Hydractinia*.

Coming next to the great series of forms which have usually been

grouped together under the name of "Perforate Foraminifera," the first family we have to deal with is that of the *Textularidæ*, in which the test may be arenaceous or calcareous, but usually possesses a perforate calcareous basis. The smaller forms of the family have a



A B

Fig. 35.—A, A specimen of *Loftusia persica*, from the Eocene of Persia, of the natural size, cut open to show its general plan of structure. (After Brady.) B, Portion of a vertical section of *Loftusia*, showing the minute structure of the test, enlarged about ten times. (Original.)

hyaline calcareous shell, with large pseudopodial foramina. The chambers are usually arranged in two or more alternating series, generally in a straight line, but sometimes in a spiral. In many cases (*e.g.*, in *Bigenerina*) the test is dimorphous, the first-formed chambers being in a double series, while the later ones are uniserial. In *Textularia* itself (figs. 29, *l*, and 36) the test is generally conical or wedge-shaped, and consists of numerous chambers arranged in two alternate parallel series. *Bigenerina* is much the same as *Textularia*, except that the last-formed segments are disposed in a single and not a double series; and both make their first appearance in the Carboniferous, the latter being a common type in many formations and being specially abundant in the Chalk. *Bulimina* (fig. 29, *n*), dating from the Trias (Rhætic) onwards, consists of spheroidal segments which progressively increase in size, and form an oblique spiral; while *Cassidulina* (fig. 29, *m*), ranging from the Miocene to the present day, though truly biserial, is more or less completely rolled up, and may thus be regarded as an involute *Textularia*. Lastly, *Chrysidalina*, dating from the Chalk, is like *Textularia*, but is triserial.

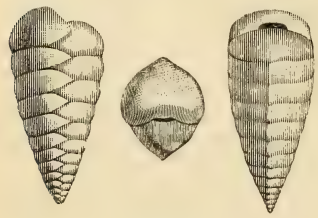


Fig. 36.—*Textularia Meyeriana*. D'Orbigny.

Closely related to the Textularians are the forms included in the small group of the *Chilostomellidæ*, in which the test is many-chambered, calcareous, and finely perforate. The segments follow

each other from the same end of the long axis, or alternately at the two ends, or in cycles of three, and the one last formed more or less completely embraces those previously formed. In *Chilostomella* itself, the segments are oval, and each entirely envelops the previous one; whereas in *Allomorphina*, the chambers alternate at three sides so as to leave portions of two, in addition to the last one, exposed to view. The former genus is confined to the Tertiary deposits, and the latter is Cretaceous and Tertiary.

The great family of the *Lagenidæ* comprises "hyaline" or "vitreous" *Foraminifera*, with a calcareous shell, the walls of which are pierced by numerous *minute* pores, and are usually more or less strikingly thin and glassy. In the compound forms of this group the successive chambers have their posterior walls formed by the front wall of the preceding segment, so that the septa are always single, instead of being double, and there is never any "intermediate" skeleton. The family may be divided into two series, *Lagena* itself being the type of the one, while *Nodosaria* is the type of the other. In *Lagena* (fig. 29, *f*) the shell is simple, flask-shaped, unilocular, with a single prominent aperture. The genus commences in the Silurian, with forms little different from, or identical with, existing types, is further developed in the Secondary and Tertiary, and is well represented at the present day. *Polymorphina* (fig. 29, *j*) is allied to *Lagena*, but it is multilocular, the chambers being usually arranged in a double series. It is represented in the Trias, and survives under common types at the present day. In the series of which *Nodosaria* is the type, we have perforate Foraminifera consisting of a succession of chambers, each of which is essentially similar to a *Lagena*, arranged in a series, which is usually nearly or quite straight, though sometimes spirally involuted. In *Nodosaria* itself (fig. 29, *g*) the chambers are simple, and are disposed in a straight line. It ranges from the Permian to the present day. *Dentalina*, ranging from the Carboniferous onwards, is fundamentally like *Nodosaria*, but the shell is bent like a bow. *Vaginulina* comprises forms similar to *Nodosaria*, but laterally compressed, and begins in the Trias (Rhætic). *Marginulina* (fig. 29, *h*) is slightly curved, or is sometimes crosier-shaped, and also starts in the Trias. *Frondicularia* (fig. 29, *i*) has the shell flattened out and leaf-like, and likewise makes its first appearance at the summit of the Trias. Lastly, *Cristellaria* (with *Robulina*) comprises forms more or less spirally inrolled or crosier-shaped, which extend from the Trias to the present day, and have a very wide development both individually and specifically.

In the family of the *Globigerinidæ*, Dr Carpenter included all those hyaline *Foraminifera*, in which the calcareous shell is perforated by large-sized pseudopodial foramina, but the group, as defined

by Dr H. B. Brady, is a much more restricted one. The test is always calcareous and perforate, and consists of a few inflated chambers arranged spirally, or of a single chamber only. There is no "supplementary skeleton," and there is a large single or multiple "general aperture" to the shell. The apparently simplest form of the *Globigerinidæ* is *Orbulina* (fig. 22), in which the test has the external form of a single globular chamber, the walls of which are perforated by a double series of foramina, large and small. It seems more than doubtful if the test, as represented in fig. 22, possesses any "general aperture." Doubt has been thrown upon the true relationships of *Orbulina* by the discovery that in many specimens, especially in those of small size, the apparently monothalamous sphere contains in its interior a young *Globigerina*-shell, attached to the inside of the wall by slender spicules. It has therefore been held that *Orbulina* is really a form of *Globigerina* in which the last chamber includes all those previously formed. The genus *Orbulina* has a world-wide distribution at the present day, and its earliest representatives appear in deposits as old as the Trias (Rhætic). The genus *Ovulites*, formerly placed in the immediate neighbourhood of *Orbulina*, appears, according to recent researches, to be in reality a Calcareous Alga. The only other member of the *Globigerinidæ* which requires notice is the type-genus *Globigerina* itself (fig. 29, *k*), in which the test is polythalamous and coarsely perforated (fig. 20). The chambers are few in number, and globose in form, and are usually arranged in a turbinate spiral, thus resembling the shell of a *Rotalia*. The chambers do not communicate with one another directly, but each opens by a special aperture into a deep central or umbilical depression. In pelagic forms (as also in *Orbulina*) the test, when perfect, appears to be covered with long and extremely delicate spines. *Globigerina* dates from the Trias, and is extremely abundant. It is of special interest, as being the principal constituent of the "ooze" (fig. 27) found at great depths in the larger oceans at the present day; while its shells form an equally large portion of the White Chalk (see p. 119).

In the large and important family of the *Rotalidæ*, the test is typically composed "of a succession of coarsely porous or globigerine segments, arranged in a turbinoid spire, and communicating with each other by a crescentic aperture situated at the junction of the septal plane with the free surface of the convolution" (Carpenter). The segments of the shell are typically so coiled that the whole of the chambers are exposed to view on the upper surface, whereas on the under side only the last convolution is visible, different types varying as to which side of the shell is the more convex. The shell-structure may be simple, but in other cases the test is

complex and is furnished with a "supplemental skeleton" and "canal-system" (fig. 21). Among the typical Rotaline forms, the genus *Discorbina*, with its coarsely porous shell, dates from the Chalk, and is found living in our seas. *Pulvinulina* (fig. 24), on the other hand, with a more finely porous shell, has been detected by Brady in rocks of Carboniferous age, and is thus one of the earliest representatives of the Rotalines. In *Rotalia* itself (figs. 21 and 29, *o*), the test is also spiral and turbinoid, but its structure is more complex than in the preceding, the shell-substance being compact and very finely porous; while each chamber is enclosed by a complete wall of its own, and there are canal-like spaces between the two lamellæ forming each septum. In these respects, *Rotalia* closely approaches the Nummuline type. The earliest *Rotaliæ* appear in the Jurassic, but the genus attains its maximum in the Tertiary period, and is well represented at the present day. The approximation to the Nummuline type is further manifested by *Calcarina* (fig. 26, B and C), in which the shell is spiral and discoidal, with spur-like marginal appendages, and with a well-developed "supplemental skeleton" and "canal-sytem." The genus has been shown by Brady to commence in the Carboniferous. In *Planorbulina* the shell is composed of numerous segments, at first spirally and then cyclically disposed. It dates from the Tertiary period, but the forms which are included under the sub-generic name of *Truncatulina* (fig. 29, *p*) commence in the Carboniferous. *Tinoporus*, dating from the Chalk, is in some respects intermediate between *Calcarina* and *Planorbulina*, its general form being like that of the former, while the irregular and partly cyclical arrangement of its chambers recalls the latter. No "general aperture" is present, but a "supplemental skeleton" and "canal-system" are developed, both of these structures being wanting in the allied *Gypsina*. Though not known in the fossil condition, the genus *Polytrema* may be alluded to here, since it has some curious resemblances to certain of the *Polyzoa*. It forms crusts, or, more commonly, branched outgrowths, parasitically attached to foreign bodies; and it consists of numerous intercommunicating irregular chambers, the walls of which are penetrated by an extensive system of capillary canals, a true canal-system being, however, absent. *Polytrema* seems to be the representative in the Rotaline series of the singular genus *Stacheia* among the *Imperforata*. Lastly, an aberrant type of the Rotalines is constituted by the genus *Spirillina*, in which the test has the form of a calcareous tube, without any internal partitions, coiled into a flat spiral, and either free or attached to some foreign body. The genus begins in the Tertiary rocks, and is represented by living forms.

Finally, we have the family of the *Nummulinidæ*, comprising the

most complex and the most highly organised of all the *Foraminifera*. In the forms included under this head, the shell is compound; the successive chambers are enclosed each in its proper wall (as diagrammatically shown in fig. 26, A); there is generally a well-developed "intermediate" or "supplemental" skeleton, which renders the shell strong and compact, and which is perforated by a "canal-system," originating in the spaces between the two lamellæ composing each septum; while the shell-substance is pierced by close-set and extremely fine tubules (fig. 37), the septa alone wanting these, so

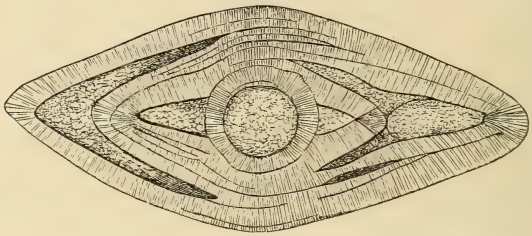


Fig. 37.—Transverse section of the test of *Nummulina pristina*, from the Carboniferous Limestone, enlarged 100 diameters, showing the primordial chamber and the tubulated shell-wall. (After H. B. Brady.)

that contiguous chambers usually communicate by but one large aperture. The lower forms of the family have a thickened and finely tubulated shell-wall, but have no intermediate skeleton. The form of the shell is typically a discoidal spiral or a cycloidal disc.

There is a relationship of a decided character between the higher Rotalines and the *Nummulinidæ*, as exhibited by forms like *Rotalia* itself, and *Calcarina* on the one hand, and by *Polystomella* and *Amphistegina* on the other hand. In *Polystomella* (fig. 29, *s*) the shell is lenticular and discoidal, and is composed of successive chambers, which are prolonged into wing-like ("alar") prolongations, which extend inwards to the centre, thus concealing the earlier turns of the spire from view, while the centre itself is occupied by a solid calcareous boss, penetrated by irregular canals. The "canal-system" is extraordinarily developed and very complex. Some of the simpler types of *Polystomella* are grouped together under the name of *Nonionina*; and the genus seems to make its first appearance in the Upper Chalk, being well represented in the Tertiaries, and surviving to the present day.

Amphistegina still more closely approaches the Rotalines, with which it has sometimes been grouped. Its shell is spiral and discoidal (fig. 29, *t*), usually more or less inequilateral, each chamber being saddle-shaped, and sending forth "alar" prolongations which reach nearly to the centre, where is placed a solid boss. The shell-substance, with exception of the septa and the central boss, is pene-

trated by numerous close-set, parallel, extremely minute tubules, but the "canal-system" is only imperfectly developed. Brady has shown that the genus occurs in the Carboniferous; but with this exception it is Tertiary and Recent.

Another very ancient, and more anomalous, type of the Nummuline group is the *Archædiscus* of Dr Brady (fig. 29, *r*), which occurs also in the Carboniferous Limestone. In this curious form the test is "convoluted, rounded, more or less unsymmetrical; formed of a non-septate tube coiled upon itself in a constantly varying direction; the shell-wall transversed by very numerous parallel minute tubuli" (Brady).

In the genus *Nummulina* itself (fig. 38) the shell is coin-shaped, of large size, sometimes as big as a florin, or larger, composed of

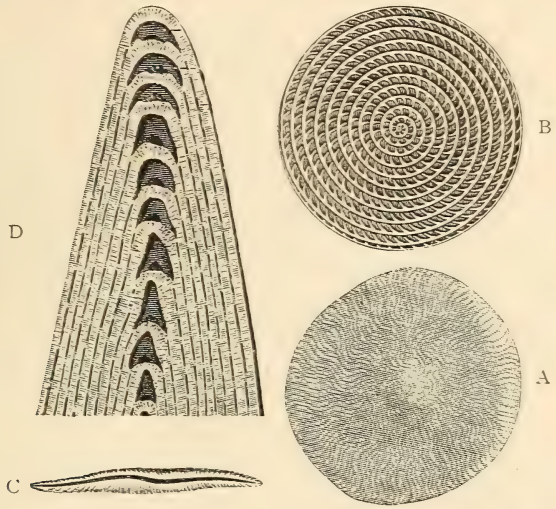


Fig. 38.—*Nummulina nummularia.* A, The shell viewed from above; B, The same horizontally bisected; C, The same vertically bisected; D, Vertical section of part of the shell, highly magnified, showing the chambers of the median plane, the alar prolongations, and the tubuli of the shell-substance. Eocene Tertiary.

numerous chambers arranged on one plane in a regular spiral. Each chamber is saddle-shaped, the internal or "alar" prolongations of each extending to the centre, so that each revolution completely encloses and conceals from view all the preceding ones. The successive chambers communicate by means of arched fissures, which perforate each septum, close to the periphery of the previous turn of the spire, while secondary and irregular pores in the septa discharge the same function. The general shell-substance is traversed by extremely minute parallel tubuli (fig. 38, D, and fig. 37); and there is

a supplemental skeleton (forming the so-called "marginal cord"), which, together with the septa, is penetrated by a well-developed and ramified "canal-system" (see fig. 26, D). By the researches of Brady, we know now that the range of the genus *Nummulina* in time must be carried back to the Carboniferous, one small form (viz., *Nummulina pristina*, fig. 37) having been detected in the Mountain Limestone of Belgium. A few "Nummulites" have also been detected in strata of Jurassic and Cretaceous age, but the maximum development of the genus is recorded in the early Tertiary period (Middle Eocene). At this period in the earth's history we find the Nummulites existing in extraordinary profusion, and building up the widespread and massive series of calcareous deposits which are known as the "Nummulitic Limestone." According to Sir Charles Lyell, "the Nummulitic Limestone, with its characteristic fossils, plays a far more conspicuous part than any other Tertiary group in the solid framework of the earth's crust, whether in Europe, Asia, or Africa. It often attains a thickness of many thousand feet, and extends from the Alps to the Carpathians, and is in full force in the north of Africa, as in Algeria or Morocco. It has also been traced from Egypt, where it was largely quarried of old for the building of the Pyramids, into Asia Minor, and across Persia, by Bagdad, to the mouths of the Indus. It occurs not only in Cutch, but in the mountain-ranges which separate Scinde from Persia, and which form the passes leading to Cabul; and it has been followed still further eastwards into India, as far as Eastern Bengal and the frontiers of China." In the later Tertiary period, the genus underwent a striking degeneration; and it is represented at the present day by only a few small forms, which are found in arctic, temperate, and tropical seas.

Very closely allied to *Nummulina*, and of equal or even greater geological importance, is the genus *Fusulina*, the typical forms of which (fig. 39) are spindle-shaped in figure, and may be compared to a Nummulite drawn out at its umbilici. According to Brady, however, some species of *Fusulina* are discoidal and symmetrical, and thus not distinguishable in *form* from *Nummulina*; while in other species the test is spherical. In internal structure, and especially in the minute tubulation of the shell-substance, the genus approaches *Nummulina*, but a regular interseptal "canal-system" appears to be wanting, and the chambers are broken up into chamberlets. Most of the *Fusulinæ* are of considerable size, often from a third to a half of an inch in length, and they often constitute massive beds of limestone, which have been justly paralleled

Fig. 39.—*Fusulina cylindrica*. Carboniferous, Russia.

with the Nummulitic Limestone of the Eocene. Thus they form whole beds of the Carboniferous Limestone in Russia, Central Europe, Armenia, India, China, Japan, and the United States. Though pre-eminently Carboniferous, they occur also in the Permian.

The remaining types of the *Nummulinida* can be merely alluded to here. The genus *Orbitoides* is extremely like *Nummulina* in external appearance and form, and has been often mistaken for it, but it differs considerably in its internal structure, and especially in the fact that its mode of growth is cyclical instead of spiral, and the place of the "alar prolongations" of the chambers of the latter is taken by a multitude of chamberlets. The genus appears first at the summit of the Cretaceous, but it undergoes, along with its ally *Nummulina*, an extraordinary development in the early Tertiary period, and it forms immense masses of Eocene limestone in the Southern United States, the West Indies, and in various parts of the Old World. A nearly allied genus is *Cycloclypeus*, which is also coin-shaped, and is strictly cyclical in its mode of growth. It occurs in the Miocene Tertiary, and the only known recent types attain an extraordinary size (over two inches in diameter). *Operculina*, again, is much more closely related to *Nummulina* proper in its internal structure, though it differs in *form*, owing to the fact that the chambers of the spirally inrolled shell have no "alar prolongations," and thus approximate to the Rotaline type. The genus commences in the Upper Cretaceous, but is particularly developed in the Eocene of the South of Europe and Africa. Lastly, *Heterostegina* (Tertiary and Recent) differs from *Operculina* chiefly in having the principal chambers broken up into chamberlets by secondary septa.

APPENDIX TO FORAMINIFERA.

Eozoön Canadense.

In connection with the subject of the *Foraminifera*, it is necessary to consider the structure and probable nature of the singular body to which the name of *Eozoön* has been given, since this body, if organic at all, must be regarded as referable to the foregoing group of organisms. There is, in fact, a special, twofold interest attaching to *Eozoön*, if it should be proved that the body so named is truly organic. In that case, *Eozoön* would, on the one hand, be the most ancient type of life which has yet been detected by the researches of palæontologists, while, in the second place, it would present us with a type of *Foraminifera* of colossal size, and in other respects of quite peculiar zoological interest. Since the whole subject of the structure and relations of *Eozoön* is one of great complexity, it would not be advisable to deal with it here in any detailed manner, or to enter into the long and still unfinished controversy which has been carried on as to the organic or inorganic nature of this remarkable body. It will be sufficient to briefly describe the general form and

mode of occurrence of *Eozoön*, the chief structural features which it presents in thin sections, and the general explanation of these features given respectively by those who regard it as Foraminiferal and those who consider it to be a purely mineral structure. In addition, it may not be out of place to indicate a few considerations based upon a prolonged and careful microscopical investigation which the present writer has independently carried out into the structure of this problematical body.

The peculiar structure which has been described under the name of *Eozoön Canadense* occurs in the crystalline metamorphic limestones of the Lower Laurentian in Canada, and it has also been detected in the same country in similar limestones believed to be of the age of the Upper Laurentian or Huronian. An allied form (species ?) has been found in rocks supposed to be Laurentian in Newfoundland; and Dr Gümbel has described a third form from crystalline limestone belonging to the "Hercynian gneiss formation" (Lower Cambrian or Huronian?) of Bavaria.

As regards its mode of occurrence, *Eozoön* appears to most commonly present itself in the form of spreading layers or confluent masses. According to Sir William Dawson, however, comparatively small, isolated specimens are found, which have a "broadly-turbinate, funnel-shaped, or top-shaped form, sometimes with a depression on the upper surface." The same observer has also described the occurrence of vertical tubes of large size traversing masses of *Eozoön*, and has compared these with the oscular canals of Sponges.

As regards its *macroscopic* characters, a mass of *Eozoön* shows a conspicuous structure out of thin alternating laminæ, arranged parallel with one another and often more or less concentrically (fig. 40). The laminæ

Fig. 40.—Fragment of *Eozoön*, of the natural size, showing alternating laminæ of loganite and dolomite. (After Dawson.)

of such a mass are usually of different colours and composition; one series being white, and composed of carbonate of lime — whilst the laminæ of the second series alternate with the preceding, are green in colour, and are found by chemical analysis to consist of some silicate, generally serpentine or the closely related "loganite," or white pyroxene. In some instances, however, according to Dawson, all the laminæ are calcareous, the concentric arrangement still remaining visible in consequence of the fact that the laminæ are composed alternately of lighter and darker coloured limestone. The calcareous layers (fig. 41, A) are composed of coarsely crystalline calcite (as viewed macroscopically), and

vary much in thickness, not only in different specimens, but commonly in different parts of the same specimen. According to Dawson, in isolated, inversely conical specimens it is the laminæ at the base which are the thickest. Very commonly, the laminæ subdivide and coalesce with one another. The serpentinous layers, which alternate with the calcareous laminæ, usually show a more or less conspicuous structure

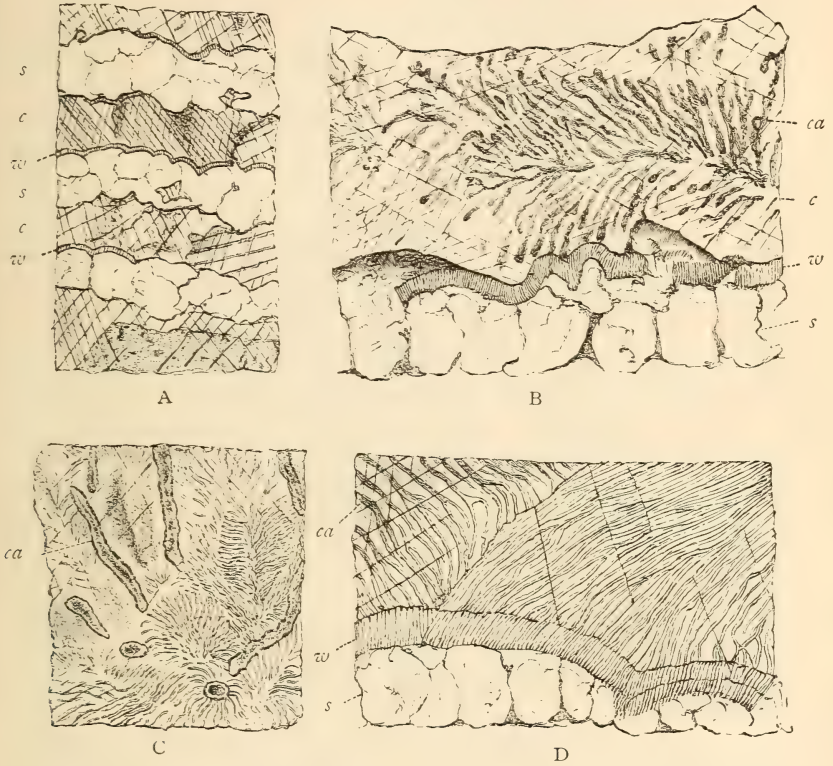


Fig. 41.—Minute structure of *Eozoön Canadense*, from the Laurentian limestones of Canada. A, Part of a vertical section of *Eozoön*, enlarged about ten times, showing the alternating layers of calcite (*c*) and serpentine (*s*); B, Part of a calcareous lamina, cut vertically, showing the "canal-system," enlarged about forty-five times; C, Part of a calcareous lamina, cut horizontally, and enlarged about sixty times, showing the large and small branches of the canal-system; D, Part of a vertical section of a calcareous lamina, enlarged about one hundred times, showing the finer divisions of the canal-system and the so-called "proper wall" (*w*). *c*, Calcareous laminæ; *s*, Serpentinous laminæ; *w*, The so-called "proper wall"; *ca*, Large branches of the canal-system. (Original.)

out of small rounded or lenticular masses. This characteristic botryoidal structure of the serpentinous laminæ is best studied in polished specimens which have been treated with weak acids, so as to dissolve out the calcareous portions of the mass to a limited depth below the surface.

As regards the *microscopic* structure of *Eozoön*, the calcareous laminæ, in well-preserved examples, exhibit a very remarkable canaliculated or

tubulated structure. In parts in which this structure is preserved, the crystalline calcite of the calcareous laminæ is seen to be traversed by branching and dendritic canals (fig. 41, B and C). Some of these canals (fig. 41, B) are of comparatively large size, and these are generally more or less extensively occupied with an infilling of serpentine, though sometimes partially filled with calcite. In connection with these large canals are much more delicate canaliculi or tubules (fig. 41, C and D), which run more or less parallel with one another, or have a tufted arrangement, and which are commonly filled with transparent *calcite*. At the edges of the calcareous laminæ these delicate and branching tubules often appear to terminate in a narrow belt or selvage (the so-called "proper wall" or "Nummuline layer" of Carpenter and Dawson), which has a transversely striated aspect, as if composed of parallel fibres or traversed by innumer-

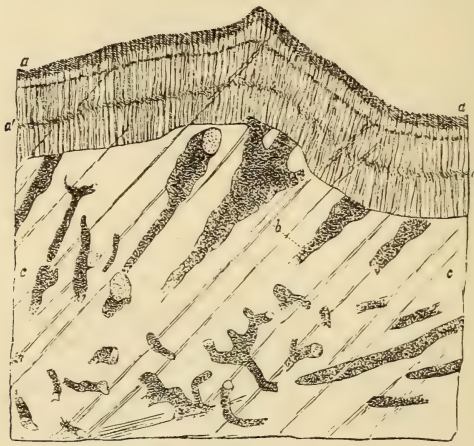


Fig. 42.—Portion of one of the calcareous layers of *Eozoön*, magnified 100 diameters. *a a*, The proper wall ("Nummuline layer") of one of the chambers, showing the fine vertical tubuli with which it is penetrated, and which are slightly bent along the line *a' a'*; *c c*, The intermediate skeleton, with numerous branched canals. The oblique lines are the cleavage-planes of the carbonate of lime, extending across both the intermediate skeleton and the proper wall. (After Carpenter.)

able minute tubuli (fig. 41, D, *w*). According to the observations of Dawson, this narrow selvage, or "proper wall," consists of "finely divided tubes, similar to those of the canal-system, and composed of its finer subdivisions placed close together so as to become approximately parallel" (fig. 42).

The actual *structure* of *Eozoön* being as above briefly described, we may in the next place shortly consider the interpretation placed upon this structure by those who regard it as organic in origin, and who, like W. B. Carpenter, Dawson, and Rupert Jones, consider it to represent an ancient type of the *Foraminifera*. Upon this view—which a reference to the subjoined diagrammatic figure (fig. 43) will render readily intelligible—the calcareous laminæ (*b b*) of a mass of *Eozoön* represent the original calcareous skeleton of a gigantic Foraminifer, while the serpentinous layers represent the successive tiers of chambers separating successive laminæ of the skeleton. The calcareous skeleton itself has been largely

crystallised or otherwise altered by the metamorphic agencies which have affected the entire mass of the enclosing rock; and the original chambers between successive layers of the shell have been filled up with serpentine or some other silicate, which has taken the place of the living matter which, to begin with, is supposed to have occupied these spaces. The serpentinous infilling has been deposited from solution in water, and has not only usually occupied the large chambers between the calcareous laminæ, but has also more or less extensively penetrated into the larger canals or even the minuter tubuli which traverse the substance of these laminæ. Placing this interpretation upon the observed structure of *Eozoön*, the central and principal portion of each calcareous lamina (fig. 43, *b b*) is regarded as corresponding with the "supplemental skeleton" of such a Foraminifer as *Calcarina* or *Nummulina*, while the branching tubes which traverse the lamina (fig. 43, *d*), are considered to represent the "canal-system" of the same. Moreover, the narrow, transversely striated band or selvage, which normally bounds each calcareous lamina above and below (fig. 43, *a a*), is regarded as corresponding with the "proper wall" of such a Foraminifer as *Nummulina*, and has therefore been commonly spoken of as the "Nummuline layer." On this view, therefore, the so-called "proper wall" is part of the actual skeleton, and the vertical lines which traverse it represent minute tubules, which open into the chambers and on the surface by correspondingly fine pores. It need only be added that if the above explanation of the observed structure of *Eozoön* be accepted, it then takes its place in the series of the *Foraminifera* as a gigantic and aberrant member of the *Nummulinidæ*, having a quite special interest and importance as both the oldest known fossil and also the largest of known Protozoans.

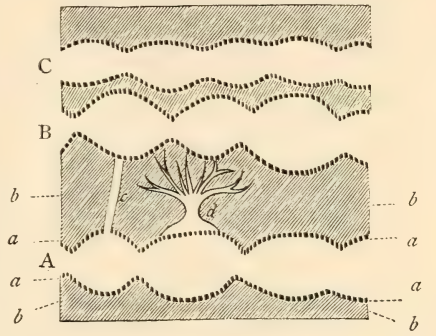


Fig. 43.—Diagram of a portion of *Eozoön* cut vertically. A, B, C, Three tiers of chambers communicating with one another by slightly constricted apertures; *a a*, The true shell-wall, perforated by numerous delicate tubes; *b b*, The main calcareous skeleton ("intermediate skeleton"); *c*, Passage of communication ("stolon-passage") from one tier of chambers to another; *d*, Ramifying tubes in the calcareous skeleton. (After Carpenter.)

On the other hand, very weighty objections have been urged against the theory of the organic nature of *Eozoön* by many observers, and more especially by Möbius in Germany and King and Rowney in Britain.

It would be out of place here to attempt to discuss these objections, but the following are, in brief, the more important arguments which have been brought forward against the organic nature of *Eozoön* and in favour of the view that it is a purely mineral structure :—

a. The structure to which the name of *Eozoön* is applied is found in highly crystalline rocks, and in parts of these which are much broken and altered. Moreover, no unquestionable organic remains have been discovered in association with *Eozoön*.

b. The general form of *Eozoön* is very irregular, and though its minute structure (supposing it to be organic) would show that it belongs to the

Foraminifera, it cannot be closely compared with any known type, recent or extinct, belonging to this group of organisms.

c. The thickness of the calcareous laminæ of *Eozoön* is not only very variable in different specimens, but is liable to great variation even in a single specimen. On the supposition, however, that the calcareous laminæ represent the layers of the skeleton of a Foraminifer or other calcareous organism, it would seem very improbable that such great variations in their thickness should be found to exist.

d. On the hypothesis of the organic nature of *Eozoön*, there is a strong *a priori* improbability of such exceedingly minute structures as the "canal-system" of a Foraminiferal test being preserved in rocks so highly crystalline as are the Laurentian limestones.

e. The canals of the so-called "canal-system" are often flat, instead of round, and are commonly unequal in point of size, while it is not unusual to find them running *obliquely* to the calcareous laminæ instead of *transversely*. These considerations would tend to show that the "canal-system" is of inorganic origin.

f. The "proper wall" is not truly tubulated, but is formed of minute parallel fibres of serpentine. It is therefore a purely inorganic structure, and is really of the nature of a vein of fibrous serpentine ("chrysotile").

Some of the above arguments against the organic nature of *Eozoön* are of a general nature, and their weight must necessarily remain largely a matter of individual judgment. Others are of a special character, and deal with matters of observation, as to which there are differences of opinion. The *special* arguments all hinge upon two points—viz., the "canal-system" and the "proper wall"—and with regard to these the following considerations may be indicated: On the view that the "canal-system" is of inorganic origin, it has usually been assumed that it consists of branched fibres of *serpentine* or of some other silicate, developed in the calcareous laminæ. The larger canals are, it is true, commonly filled with serpentine, but it admits of demonstration that the smaller canals are commonly, and in fact usually, occupied simply by *crystalline carbonate of lime*. On this point, the author is able to fully corroborate the observations of Carpenter and Dawson. In the second place, it can be proved that the so-called "proper wall" of *Eozoön* is, as a rule, *calcareous*, and that it cannot, therefore, be regarded as universally of the nature of fibrous serpentine (chrysotile). This can be best shown by acting with acids on thin vertical sections of *Eozoön* along a narrow transverse band, leaving the two ends of the section untouched. When this is done, it is found that along the narrow tract acted upon by the acid, not only have the calcareous laminæ been dissolved out, but the so-called "proper wall" *has at the same time also disappeared*, its composition out of carbonate of lime being thus conclusively proved. In some cases, the "proper wall" does not appear to be wholly destroyed by acids, and in such cases it may be supposed that the tubuli of this structure have been injected with serpentine, and have thus been enabled to resist the action of the solvent. The above observation, at any rate, appears to show conclusively that the so-called "proper wall" cannot be *always* of the nature of a layer or vein of fibrous serpentine (chrysotile), since it is very commonly and quite unquestionably soluble in weak acids. At the same time, true chrysotile veins often intersect masses of *Eozoön*, and it is quite probable that in some instances such veins have been confounded with the peculiar striated selvage to the calcareous laminæ of *Eozoön*, which is really what should be understood as the "proper wall."

Upon the whole, therefore, it would appear that the much-vexed question of the true nature of *Eozoön* is still incapable of receiving its final solution. It is clear that in any endeavour to solve this problem only the *best* specimens—those, namely, which possess the so-called "canal-system" and "proper wall" in a well-preserved state—can be taken into account; since it is one of the most ordinary experiences of palæontologists to find that out of a series of specimens of some quite indubitable fossil—such as a coral—only a very limited number retain their internal structure in a recognisable condition. It is also a reasonable argument that until mineralogists or petrologists are able to point in some unquestionable mineral or rock to a structure strictly comparable with the "canal-system" of *Eozoön*, they are not entitled to assert positively that the latter has a purely inorganic origin. Lastly, some weight must be attached to the argument that though *analogous* structures (banded rocks of various kinds) are known, nothing clearly inorganic has yet been discovered the general structure of which can be regarded as precisely parallel with that of *Eozoön*.

In connection, finally, with the subject of *Eozoön*, it may be noticed that Sir William Dawson has given the name of *Archæosphærinæ* to small spherical masses of serpentine, sometimes single, sometimes united together in small numbers, which he finds in the Laurentian limestones of Canada, and which he states to be surrounded by a tubulated calcareous shell, resembling the "proper wall" of *Eozoön*. He is of opinion that these bodies are either detached chamberlets of *Eozoön*, or that they are independent organisms, allied to *Eozoön*, but of a simpler type.

CHAPTER IX.

PROTOZOA — Continued.

Radiolaria.

The order of the Radiolarians comprises a vast number of Rhizopods, in which *the sarcode-body consists of a central protoplasmic mass, enclosed in a porous, membranous, or chitinous capsule, which is in turn surrounded by a thick layer of sarcode. The intra-capsular sarcode contains a central "nucleus," and the pseudopodia* (fig. 44) *have the form of slender radiating filaments, which rarely anastomose with*

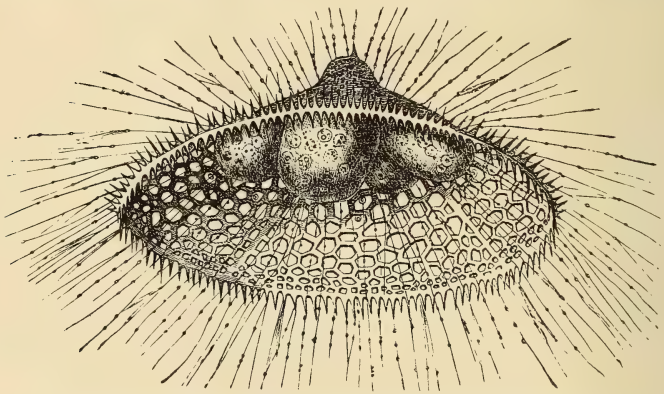


Fig. 44.—*Eucecryphalus Schultzei*, with the pseudopodia extended, showing the perforated siliceous test and the lobed protoplasmic body. (After Kölliker.)

one another. As a rule, the protoplasmic body secretes a radially disposed skeleton composed of silica, of a silicate, or of a horny substance ("*acanthin*").

As regards the *skeleton* of the Radiolarians, some forms (*Thalassicolla, Thalassolampe, Collozoum*, &c.) are wholly devoid of hard

structures. Moreover, among those types in which a skeleton is developed, there are great differences as regards both the chemical composition and the structure of this. As regards the first of these points, the skeleton is never calcareous, but presents itself under one or other of the following three modifications. In the first place, the skeleton may be composed of pure silica. This is the case in the *Polycystina* (the *Spumellaria* and *Nassellaria* of Haeckel), which constitute the largest and most typical group of Radiolarians. In another series of forms the skeleton is a compound of silica with some organic compound, or is a "silicate of carbon" (Haeckel). This occurs in the entire group of the *Phæodaria*, except in *Dictyocha* and its allies. Lastly, in a third series of forms the skeleton consists of a peculiar organic substance ("acanthin") allied to chitine or horn. The forms in which the skeleton is of this nature are grouped together by Haeckel under the name of *Acantharia*.

As regards the *form* of the skeleton, the most usual type is that of a latticed shell (fig. 45), enclosing the central capsule. In certain Radiolarians, however, the skeleton consists of radially or tangen-

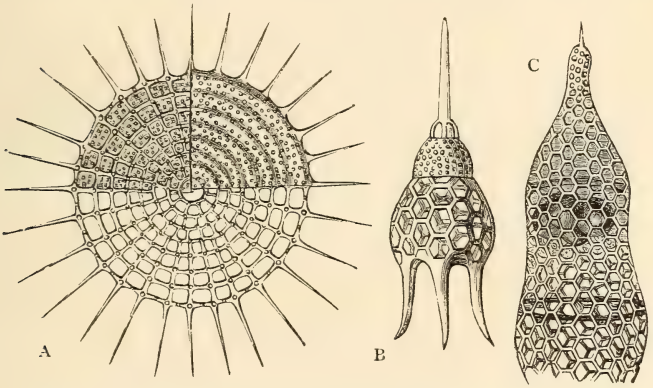


Fig. 45.—Skeletons of *Polycystina*. A, *Stylodictya multispina*; B, *Podocyrtis Schomburgii*; C, *Eucyrtidium lagena*. (After Haeckel.)

tially disposed spicules; or it may have the form of a simple ring, or of a "basal tripod with or without a loose tissue of trabeculæ" (Haeckel). In the *Polycystina* (*Spumellaria* and *Nassellaria*), the siliceous bars of the skeleton are invariably solid, whereas in the *Phæodaria* the parts of the skeleton are always hollow.

As regards their *classification*, Professor Haeckel raises the Radiolarians to the rank of a distinct *class* of the *Protozoa*, and he divides them into the following four legions or sub-classes :—

1. SPUMELLARIA.—Capsular membrane perforated by innumerable fine pores. Fundamental form originally spherical. Skeleton siliceous, or

in some cases absent. No dark pigment-body ("phæodium") in the extra-capsular sarcode.

This division includes forms such as *Thalassicolla* and *Collozoum*, in which the skeleton is wanting, with others having a skeleton of siliceous spicules, and with a large number of the forms usually spoken of as "*Polycystina*" in which the skeleton has the form of a latticed siliceous shell.

2. ACANTHARIA.—Capsular membrane perforated by numerous fine pores. Fundamental form originally spherical. Skeleton composed of "acanthin." No dark pigment-body in the extra-capsular sarcode. This group includes forms such as *Acanthometra* and its allies.

3. NASSELLARIA.—Capsular membrane perforated by a porous area, or by one single large opening divided into numerous very fine pores. Fundamental form originally egg-shaped. Skeleton siliceous. No dark pigment-body ("phæodium") in the extra-capsular sarcode. This group comprises all those "*Polycystina*" which are not included under the head of *Spumellaria*.

4. PHÆODARIA. — Capsular membrane double, perforated by one simple main opening prolonged into a tube, commonly with one or two small accessory openings. Fundamental form originally egg-shaped. A dark pigment-body ("phæodium") is constantly present in the extra-capsular sarcode. The skeleton is siliceous, being usually composed of a compound of silica with some organic substance, but in other instances (*Dictyocha*) consisting of pure silica.

As regards their *distribution in space*, the Radiolarians are exclusively marine, and are found in all seas and at all depths. They are commonly floating organisms, and are often present in enormous numbers, the greatest variety of specific types, however, being found in the warm seas of the tropics. Many Radiolarians are "pelagic," and inhabit the surface-waters of all oceans; others are "abyssal," and are confined to great depths in the sea; while others, again, are "zonarial," and are restricted to particular bathymetrical horizons between the surface and the bottom. Over large areas of the deep sea, principally at depths of from two thousand to over four thousand fathoms, the bottom is found to be covered with extensive deposits of "Radiolarian ooze." The deposit so called is a siliceous mud, with little calcareous matter, which is composed more or less largely of the siliceous tests of various Radiolarians. The skeletons of Radiolarians are, however, also present, in smaller or greater numbers, in many of the marine deposits which are formed at comparatively limited depths.

As regards their *distribution in time*, the Radiolarians are abundantly represented by fossil forms, and are now known to have a high antiquity. Owing, however, to the vast number of forms included in the *Radiolaria*, and the great complexity of their classification, the study of the fossil types can hardly be undertaken except by a specialist. For these reasons, nothing further will be here attempted than merely to give a brief outline of the more important facts relating to the past history of the *Radiolaria*. The student

desirous of fuller information, or anxious to study the fauna of any particular Radiolarian deposit, will of necessity consult the works of Ehrenberg, Rüst, Haeckel, and others, who have specially devoted themselves to the study of these minute organisms.

As regards the past history of the great groups of the Radiolarians, the *Acantharia*, in which the skeleton is composed of "acanthin," are wholly unknown in the fossil condition. This is likewise the case with the group of the *Phæodaria*—in which the skeleton is composed of silicate of carbon—with the single exception of the small group represented by *Dictyocha* and its allies, in which the skeleton is purely siliceous. In *Dictyocha* (fig. 46, *d*), the skeleton is composed of irregular bars of flint united into a loose network with wide meshes. The genus begins in the Upper Chalk, and is represented in Tertiary deposits and in recent seas.

With the above-noted exception, all the known fossil Radiolarians belong to the group of the so-called "*Polycystina*," comprised in the two divisions defined by Haeckel under the names *Spumellaria* and *Nassellaria*. In all of these forms the skeleton is purely siliceous, and it usually has the form of a porous latticed shell, the precise shape of which varies in different types.

Until recently, Radiolarians had only been detected in the fossil condition in deposits of Kainozoic and Mesozoic Age; and our knowledge of Palæozoic types of Radiolarians is still very incomplete. According to Haeckel, however, Dr Rüst (whose researches on this subject are still unpublished) has discovered various types of *Polycystina*, "of very simple form and primitive structure," in rocks as old as the Silurian, or even the Cambrian. The remains of Radiolarians have also been indicated as occurring in the Carboniferous Limestone of England, but the true nature of these has not been clearly established.[1]

Radiolarian remains have now been discovered in all the great Mesozoic systems. From the Jurassic system, in particular, numerous fossil *Polycystina* have been described by Zittel, Dunikowski, and Rüst. A noticeable Jurassic genus is *Cœnosphæra*, which is also found in the Chalk, in the Miocene marls of Barbados, and in recent seas, and which has relationships with *Collosphæra*. Many of the Jurassic Radiolarians occur in jasper, flint, or chert; but they are especially abundant in what have been termed "Radiolarian quartzes." These are cryptocrystalline quartzites or hard siliceous rocks, which are composed "for the most part of the closely compacted shells of *Spumellaria* and *Nassellaria*" (Haeckel). The

[1] Considerable portions of the Carboniferous Limestone of Britain are occasionally partially composed of the minute calcareous spheres which have been described under the name of "*Calcisphæræ*." These enigmatical bodies are now composed of carbonate of lime; but it has been conjectured that they were originally siliceous, and that they are really referable to the *Radiolaria*.

jaspers with Radiolarians are considered by Haeckel as of the nature of true "silicified deep-sea Radiolarian ooze." Many forms of Radiolarians have also been yielded by the so-called "Radiolarian coprolites" of the Lias of Hanover. These are "roundish or cylindrical bodies, which may attain the size of a goose-egg; they probably originated from Fish or Cephalopods, which had fed upon Crustacea, Pteropoda, and similar pelagic organisms, whose stomachs were already full of Radiolarian skeletons" (Haeckel).

The Radiolarians which have hitherto been discovered in the Cretaceous rocks are few in number, but Zittel has described several

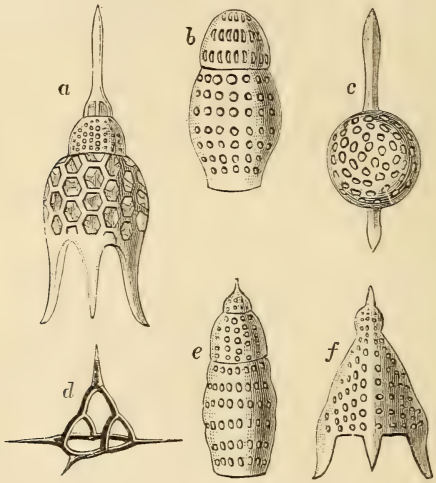


Fig. 46.—Types of Polycystina. *a, Podocyrtis Schomburgii; b, Dictyomitra Montgolfieri; c, Haliomma dixiphos; d, Dictyocha Messanensis; e, Eucyrtidium elegans; f, Lychnocanium lucerna.* *d* is living, and is after Haeckel; the remaining are Tertiary, and are after Ehrenberg. All the figures are greatly enlarged.

species from the Upper Chalk of Germany. The Cretaceous genera *Dictyomitra* (fig. 46, *b*) and *Stylodictya* (fig. 45, A) are represented in both Tertiary and recent seas.

In formations belonging to the Tertiary period, Radiolarians are found in vast abundance in certain deposits (marls and clays), which may be regarded as "fossil Radiolarian oozes." These Tertiary Radiolarian clays and marls appear to be very widely distributed, but the most famous of these deposits is the Polycystine Marl of Barbados, the age of which is Miocene. The so-called "Barbados earth" is a friable, earthy or chalky marl, which rises to heights of over 1000 feet above the level of the sea, and is more or less extensively composed of the shells of Radiolarians, with a variable proportion of the calcareous tests of the *Foraminifera*. According

to Haeckel, the number of species of Radiolarians in the Barbados earth is not less than four hundred, and is probably more than five hundred. This eminent authority regards the Barbados earth as a deep-sea deposit, and states that very many of the Barbados Radiolarians "are to-day extant and unchanged in the Radiolarian ooze of the deep Pacific Ocean."

Very similar to the Barbados earth is the Polycystine marl or "tripoli" of Sicily, Calabria, Greece, and Northern Africa, the age of which is also Miocene. Another deposit of the same nature is the tripoli or Radiolarian clay of the Nicobar Islands, which rises to elevations of about 2000 feet above the level of the sea, and is probably of Miocene or Oligocene age.

Of the more common Tertiary genera of Radiolarians, *Haliomma* (fig. 46, *c*), *Heliodiscus*, *Actinomma*, and *Didymocyrtis* belong to a group of forms in which the skeleton consists of two, three, or more porous spherical shells, included concentrically within one another, the smaller within the larger, and united by radial bars. In other cases, as in the genera *Podocyrtis* (fig. 46, *a*), *Eucyrtidium* (fig. 45, c), *Lychnocanium* (fig. 46, *f*), and *Dictyomitra*, the skeleton has the form of a latticed shell, which may be undivided, or is partially marked off into two or more compartments by transverse constrictions. The two poles of the shell in these cases are quite unlike each other, and the membranous capsule of the living animal is included within the closed apical pole. In other cases, again, the skeleton consists of a flat, or lenticular and biconvex plate, which is sometimes double, and has a more or less complex internal structure. This type of skeleton is found in such genera as *Astromma*, *Trematodiscus*, *Rhopalastrum*, *Stephanastrum*, and *Stylodictya* (fig. 45, A).

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CHAPTER X.

SUB-KINGDOM II.—PORIFERA.

Under the name of *Porifera* are included all those singular organisms which are commonly known as Sponges. Originally regarded as being of a vegetable nature, the Sponges are now universally admitted to be animals; though naturalists are not yet in absolute agreement as to the precise position in the animal kingdom which ought to be assigned to them. Owing to the close likeness of some of the cell-elements of the Sponges to certain of the *Protozoa*, the entire group has been often referred to this latter sub-kingdom. Thus, some of the cells of a sponge are morphologically identical with the *Amœbæ*, while others present the closest possible resemblance to the Flagellated *Infusoria*. Hence, a sponge has often been regarded as being a kind of colony, the units of which are morphologically Protozoans. Naturalists are, however, now agreed as to the removal of the Sponges from the *Protozoa;* and they are by many authorities regarded as forming the lowest division of the Zoophytes (*Cœlenterata*). Other authorities consider that the Sponges represent a distinct morphological type, intermediate between the *Protozoa* and the *Cœlenterata*, and that they are therefore entitled to take rank as a separate sub-kingdom, to which the name of *Porifera* has been given. In the present state of our knowledge, this view seems to be the one which is attended with the fewest difficulties, and it will therefore be followed here.

The Sponges may be defined as *multicellular organisms of variable shape, the cells of which are typically disposed to form an outer membrane, an inner membrane, and an intermediate stratum; and which are traversed by canals, which open on the surface, and which are more or less extensively lined by flagellate cells. In most cases the cellullar aggregate is supported by a framework of horny fibres, or of flinty or calcareous spicules. A definite mouth and stomach are wanting, and a nervous system is not known with certainty to be developed.*

The entire aggregate of cells which constitutes a sponge is so

arranged as to be traversed by a series of canals, which convey water in and out of the organism, and which are thus connected with respiration and the procuring of food. Looking at the skeleton of a dried sponge, the most obvious sign of the existence of this "aquiferous system" is the presence of one or more large superficial openings, together with a great number of much smaller apertures (fig. 47,

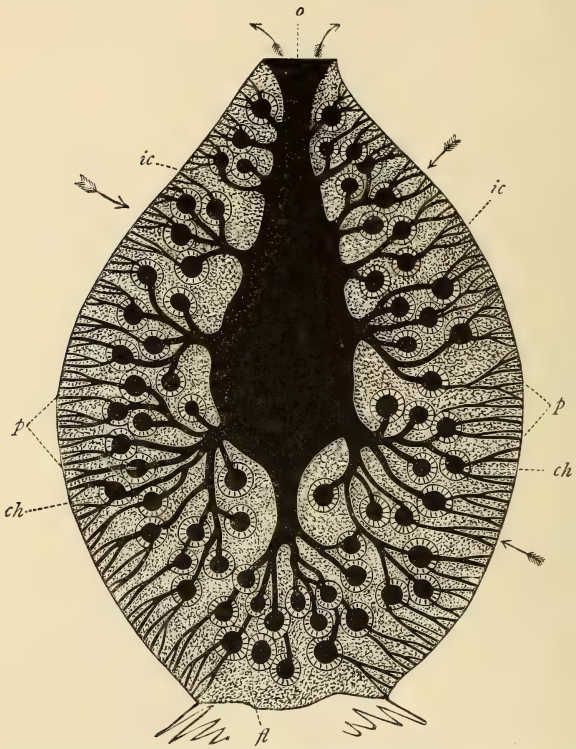


Fig. 47.—Diagrammatic representation of the structure of a simple Sponge, as seen when cut in half vertically. The general "sponge-flesh" is lightly shaded (*fl*); the canal-system is black, and the arrows show the course of the water-currents. *p p*, "Pores," opening into "inhalant canals," which conduct to the "ciliated chambers" (*ch*). From these chambers proceed the larger "exhalant canals" (*ic*), which open into a general central space or "cloaca." This space terminates on the surface by a single large opening or "osculum" (*o*), which serves for the exit of the water. (After Haeckel)

p p). These latter are termed the "pores," and though permanently present in the skeleton, they are only temporarily present in the soft parts, being produced afresh, when required, as openings between the sponge-bells of the ectodermal layer. The "pores" (fig. 47, *p p*) open directly, or through the intervention of more or less extensive subdermal cavities, into a series of canals, which ramify in

every direction through the sponge, and which are called "inhalant canals," as it is through these that the water is conveyed to the interior of the sponge. The "inhalant canals" ultimately open into a second series of canals, which converge to form one or more large tubes which open on the surface by a corresponding number of large openings. These large tubes (fig. 47, *ic*) carry the water out of the organism again, and they are hence called "exhalant canals"; while their surface-openings are known as the "oscula." The "oscula," though capable of being temporarily closed, are permanent, and are often placed on chimney-like elevations. If there should be but one osculum, it is placed at the apex of the sponge (fig. 47, *o*), while the pores occupy the general external surface. What is commonly called a "sponge" may consist of only a single excretory opening or "osculum," together with the "pores" belonging to this (fig. 47); or it may consist of a larger or smaller number of such "oscula," each with its proper complement of "pores." In the latter case, each osculum, with its accompanying pores, constitutes a "person," and the entire organism is known as a "sponge-stock."

In a living sponge, in its active condition, a circulation of water is kept up throughout the organism by means of this system of canals. The water is admitted from the exterior by the pores, and is driven through the deeper parts of the sponge by means of flagellate cells, which line a series of globular chambers developed between the inhalant and the exhalant canals (fig. 47, *ch*). From these "flagellated chambers" the water is driven into the exhalant canals, and finally escapes again by the osculum or oscula. In this way, the separate sponge-cells are enabled to carry on their nutritive and respiratory processes.

In a few sponges (the *Myxospongiæ* of Haeckel) there is no skeleton, and the above description would, therefore, fully express the general structure of the organism. In the vast majority of sponges, however, the soft cellular body is supported by more or less extensively developed hard structures, which collectively constitute the *skeleton*. The nature of the skeleton varies greatly in different forms, and these variations have been largely made use of in the identification and classification of the Sponges. Speaking generally, the skeleton has the form of a more or less coherent framework, composed either of horny fibres, or of needles of mineral matter, or of both these elements in combination. The different modifications of the skeleton will be more particularly spoken of in dealing with the different groups of sponges. It will be sufficient to point out here that, apart from modifications in the *form* of the skeletal elements, there are the following four principal types of skeleton among the Sponges:—

1. In certain sponges (such as the Common Bath Sponges) the skeleton (fig. 48, A) is wholly composed of netted horny fibres, without proper "spicules." The substance composing the fibres in such

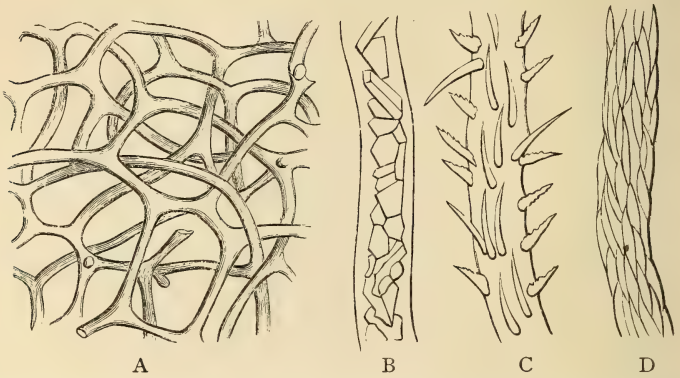


Fig. 48.—Forms of the skeleton in the fibrous Sponges. A, Horny, non-spiculate skeleton of the Bath Sponge, enlarged about fifty times; B, Horny fibre cored with sand-grains; C, Horny fibre with projecting siliceous spicules ("Echinonematous" Sponge); D, Fibre in which the spongin has been more or less completely replaced by siliceous spicules ("Holorhaphidote" Sponge). B, C, and D are greatly enlarged, and are after Carter.

types is allied to horn, but not precisely of the same nature, and it is known as "spongin" or "keratode."

2. In another group of sponges, including most of the commoner forms, the skeleton is more or less extensively composed of siliceous

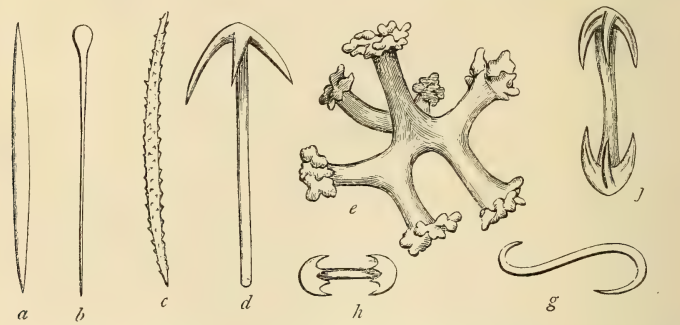


Fig. 49.—Spicules of Sponges. *a*, Monactinellid skeleton-spicule of *Reniera*; *b*, Monactinellid spicule of *Cliona*; *c*, Monactinellid spicule of *Spongilla*; *d*, Tetractinellid skeleton-spicule of *Geodia*; *e*, Skeleton-spicule of a Lithistid Sponge (*Ferea*); *f*, Flesh-spicule of *Cribella*; *g*, Flesh-spicule of *Esperia*; *h*, Flesh-spicule of *Hyalonema*. All the figures are greatly enlarged. (After Schmidt, Vosmaer, Zittel, &c.)

needles or "spicula," of various forms (fig. 49). These spicules may be embedded in various ways in a reticulated fibrous skeleton of spongin (fig. 48, C); or the horny material may be greatly reduced,

so that the skeleton-fibre consists essentially of minute flinty needles (fig. 48, D).

3. In a third group of sponges, the skeleton is destitute of horny matter, and consists wholly of siliceous spicules, which may be fused with one another into a continuous framework, or may be so interlocked by their ends as to produce practical rigidity, or may be simply held in position by the fleshy substance of the sponge. In both this group and the preceding, in addition to the spicules of the proper skeleton, there are generally developed in the mesoderm numerous still more minute microscopic needles of flint, which are known as "flesh-spicules."

4. Lastly, there is a group of sponges in which the skeleton is wholly made up of spicules of carbonate of lime.

In all sponges which possess hard structures of flint or lime, the "spicules" consist, each, of concentric layers of mineral matter deposited round a central fibre of organic matter which occupies an "axial canal" in the spicule. In the *Calcispongiæ* each spicule may be regarded as essentially a single crystal of carbonate of lime. In the ordinary recent siliceous Sponges, on the other hand, the spicules are composed of colloidal silica, which is as clear as glass, wholly non-crystalline, and entirely unaffected by polarised light between crossed Nicols. The silica of recent sponge-spicules is also soluble in hot solutions of caustic potash.

As regards the *distribution* of the Sponges *in space*, the great majority are marine, but representatives of the *Spongillidæ* are found in fresh waters in all the great continental regions except Australia. Of the marine Sponges, the *Calcispongiæ* and *Ceratospongiæ* are principally inhabitants of shallow water. On the other hand, the Hexactinellid Sponges are mostly found in deeper water, the majority living at depths of from 100 to 2500 fathoms. The Lithistid Sponges, on the contrary, are found in comparatively shallow water, being most abundant between depths of 10 to 150 fathoms.

In connection with the subject of the *distribution in time* of the Sponges, it is necessary to briefly consider the different modes in which the skeleton of the Sponges may be preserved in the fossil condition. Taking first the Sponges which secrete a siliceous skeleton, it has been pointed out above that the silica of the spicules or spicular network of these, in the *recent* condition, is colloidal and non-crystalline, glassy, and entirely unaffected by polarised light. Though unaffected by acids, the spicules undergo solution in hot caustic potash, and there is reason to know that they readily become changed, or even dissolved, under certain natural conditions which it is difficult or impossible to imitate in the laboratory. While the above is the condition of the siliceous spicules in recent Sponges, these structures in fossil Sponges have, as a rule, undergone more or less change during the process of fossilisation, the following being the principal forms of alteration which have been observed.

(*a.*) The silica of the spicules may be changed into an amorphous

condition. The alteration is in this case but slight, since the silica is still in the colloidal state, and the principal change that has occurred is that the spicules have lost their original glassy aspect, and have become porcellanous and milky-white when viewed by reflected light.

(*b.*) The silica of the spicules may have become cryptocrystalline or crystalline. In this form of alteration, the original colloidal silica of the spicules has become changed into chalcedony or quartz, and the spicules now exhibit with polarised light the same colour-changes as are shown by the above minerals.

(*c.*) In a great many cases among fossil Sponges, the original flinty skeleton has undergone more or less complete solution during fossilisation, the Sponge being now represented only by hollow casts of the original skeleton in the matrix of the enclosing rock. In the case of calcareous organisms it has long been well known to palæontologists that the skeleton very commonly undergoes solution, leaving nothing but a hollow mould or impression in the rock to mark its former existence. Silica being a much more stable substance than carbonate of lime, it used to be supposed that an originally flinty skeleton would not be liable to undergo a similar solution. It has, however, been conclusively shown by Zittel, Sollas, and Hinde, that this supposed stability of organic silica is largely imaginary. According to the last-named observer, "it may be accepted as proved that silica in the colloid state, in which it occurs in the skeleton of recent siliceous Sponges, and also in the original condition of fossil Sponges, is extremely liable to chemical changes, and that it is only when it is in the condition of chalcedony, or is crystalline, that it can be regarded as stable. The changes in the siliceous skeletons of fossil Sponges, mentioned above, show the tendency of the silica to pass from the unstable colloid to the stable chalcedonic or crystalline condition. Under favourable conditions this chemical change has taken place without destroying the form of the spicular skeleton, but in other circumstances the colloid silica of the skeleton has been wholly dissolved away, and redeposited, usually in the chalcedonic condition, so as to form solid beds of chert and bands of nodular flints."

(*d.*) In the cases just spoken of, the original siliceous skeleton of the Sponge has undergone solution, and there is left in the rock a hollow mould of the skeleton, this mould being commonly so accurate as to preserve with fidelity the form of the component spicules of the skeleton. Very usually, however, the mould thus formed becomes ultimately completely filled up with some mineral substance deposited from the water which percolates through the rock; the result being the formation of a "pseudomorph" of the original Sponge, or, in other words, a body which has the exact form, and may even have the microscopic structure, of the original Sponge, but which consists of some secondary substance which has taken the place of the original skeleton. The substance which has in this way replaced the original Sponge is most commonly crystalline calcite, but peroxide of iron is likewise often the replacing material, or, less commonly, iron-pyrites or glauconite; while in some cases it would appear that the replacing substance has been chalcedonic silica. It only needs to be added in this connection that the changes above spoken of do not necessarily affect an entire Sponge, but that specimens often occur in which a portion of the skeleton has been fossilised in one way, while another part may have been preserved in a different manner.

The *Calcispongiæ* do not, as a rule, undergo fundamental alteration, as regards their skeletal structures, during fossilisation. In some late

deposits, the spicules of Calcareous Sponges are found in a condition not recognisably different from that of recent examples. As a rule, "the spicular fibres of fossil Calcisponges retain their original structure of carbonate of lime, though the form of the component spicules has to a large extent disappeared, and the fibres are now either of crystalline grains of calcite or show a finely radiate prismatic structure" (Hinde). In certain cases, however, the calcareous skeleton of a Calcisponge may be found to be replaced, as occurs commonly in the case of Corals and other calcareous organisms, by chalcedonic silica. Such "silicified" specimens have necessarily undergone an entire destruction of the minute structure of the skeleton, though the *form* of the skeleton may be perfectly well preserved.

As regards their general *geological distribution*, the Sponges are very largely represented in past time, and have a very high antiquity. The two recent groups of the *Myxospongiæ* and *Ceratospongiæ*, being devoid of hard parts or having only a horny skeleton, are unknown in the fossil condition, though doubtful examples of the latter have been brought forward. The Sponges with a skeleton of siliceous spicules are known to occur in deposits as ancient as the Cambrian, the oldest Sponge at present known being the *Protospongia fenestrata* (fig. 50) of the Menevian Slates of St David's, South Wales. In strata of Ordovician age the remains of Sponges are not very uncommon, the groups of the *Lithistidæ* and *Hexactinellidæ* being both represented, the former by types like *Hindia*, and the latter by *Hyalostelia*, *Receptaculites*, and *Ischadites*. In the Silurian deposits the same groups of Sponges are well represented by forms such as *Aulocopium*, *Astylospongia*, and *Dictyophyton;* while the group of the Monactinellid Sponges is represented by the genus *Climacospongia*. If we except the aberrant group of the *Receptaculitidæ*, the Devonian system has, so far, proved to be singularly barren of Sponge remains, though a few types (*Astræospongia*, *Dictyophyton*, &c.) have been detected in strata of this age. On the other hand, the seas of the Carboniferous period were tenanted by a vast abundance of Sponges, belonging to few generic types—so far as yet known—but representing the distinct groups of the *Monactinellidæ*, *Tetractinellidæ*, *Lithistidæ*, *Hexactinellidæ*, and

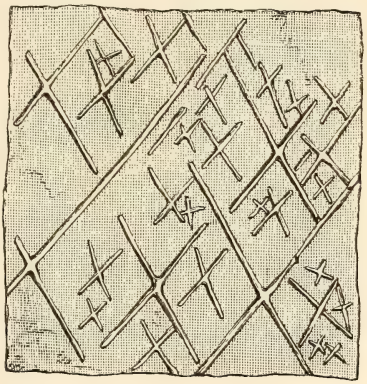


Fig. 50.—Part of the spicular mesh of *Protospongia fenestrata*, enlarged five diameters, from the Menevian strata of South Wales. The spicules are slightly distorted by cleavage. (After Hinde.)

Heteractinellidæ. So great was the profusion of Sponge-life during Carboniferous times that thick beds of chert—as conclusively demonstrated by Hinde—were formed by the gradual accumulation of siliceous spicules on the floor of the sea. These siliceous sponge-beds are largely developed in the Carboniferous limestone and Yoredale beds of the North of England, Wales, and Ireland, and may reach a thickness of more than fifty feet [in Ireland, a maximum thickness of over 300 feet of these chert-beds has been observed]. The highest Palæozoic deposits—viz., the Permian—have hitherto yielded few or no unequivocal remains of Sponges.

Coming to the Mesozoic deposits, the Trias has not yielded a large number of Sponges, and the great majority of the known forms of this period belong to the *Calcispongiæ*, and are referable to the extinct group of the *Pharetrones*. On the other hand, an enormous number of Sponges are known to occur in strata of Jurassic age, almost all the hitherto recognised types of this period belonging to the three groups of the *Lithistidæ*, *Hexactinellidæ*, and *Pharetrones* (*Calcispongiæ*). At the summit of the Jurassic system (in the Purbeck beds) we also meet with the first undoubted representative of the fresh-water genus *Spongilla*. In the Cretaceous system, and especially in its upper division, Sponges also occur in vast numbers, the three groups above mentioned being those most largely represented. It is noticeable, however, that the aberrant Calcisponges which form the group of the *Pharetrones* diminish in numbers towards the close of the Cretaceous period; while the groups of the *Monactinellidæ* and *Tetractinellidæ* have a fair representation. In parts of the Cretaceous system, and particularly in the Lower and Upper Greensand, occur beds of siliceous rock, which have been shown by Hinde to have been formed by the accumulation of the microscopic spicules of various types of Sponges. In some cases, these spicules are loosely compacted together, and give rise to a porous siliceous rock. More commonly, however, the spicules have undergone partial solution in sea-water, and the dissolved silica thus obtained has been subsequently redeposited, and has formed a siliceous cement which has bound together the undissolved spicules in a general cherty matrix. In such cases, the true nature of the rock can only be recognised by an examination of thin sections (fig. 51) under the microscope.

There is, further, every reason to believe that the nodular flints which form such a striking feature in the White Chalk have been in reality produced by the solution of the skeletons of flinty Sponges and other siliceous organisms, and the subsequent redeposition of the silica thus obtained in a solid form. It is well known, namely, that the siliceous Sponges of the White Chalk have usually had their original siliceous skeleton more or less wholly dissolved out,

the original skeleton being now represented either by empty casts in the rock or by pseudomorphs of lime, peroxide of iron, or iron-pyrites. The general freedom of the body of the White Chalk from silica can thus be readily explained on the ground that the siliceous organisms which it, to begin with, contained, underwent a more or less complete solution. The dissolved silica thus obtained must, however, have been from time to time redeposited in a solid form, thus giving rise to the nodules of flint which are so largely disseminated through parts of the White Chalk. On this view, the silica of the Chalk-flints had an organic origin, though deposited from solution in sea-water. On this view, it is also possible to account for the fact that the silica, in course of redeposition, should not only have accumulated in a nodular form round any foreign bodies which may have been lying on the sea-bottom at the time, but should also have commonly penetrated into the internal cavities of organic bodies, or should even have given rise to tabular masses or to actual veins.

Fig. 51.—Section of chert from the Upper Greensand, showing numerous sponge-spicules embedded in a chalcedonic matrix, enlarged forty diameters. (After Hinde.)

In deposits of Tertiary age, finally, remains of Sponges have hitherto been detected in much smaller numbers than in the preceding Mesozoic strata. The great group of the *Pharetrones* among the *Calcispongiæ* seems to have become extinct with the close of the Cretaceous period, and the Hexactinellids and Lithistids are for the most part but poorly represented. In the Miocene strata of Algeria, however, Pomel has described an abundant fauna of Hexactinellid and Lithistid Sponges.

CHAPTER XI.

PORIFERA—Continued.

Classification and Principal Groups of the Sponges.

There is, perhaps, no single group of the animal kingdom in which it has proved so difficult to establish a natural classification, as has been found to be the case with the Sponges. Even at the present day there is no extant classification which can be regarded as final. It is, however, now generally admitted that the calcareous Sponges are so far separated from all the other groups of Sponges as to properly constitute a distinct *class* of Sponges. The non-calcareous Sponges may be grouped together in a second class under the name of *Plethospongiæ*, proposed for them by Professor Sollas. As regards the ordinal divisions of the *Plethospongiæ*, the grouping followed by Professor Zittel may be adopted, with some modification, and the general classification of the Sponges is thus expressed in the following table :—

SUB-KINGDOM PORIFERA.

Class I. Plethospongiæ (Sollas).

Order 1. Myxospongiæ (*Halisarca*).
„ 2. Ceratospongiæ (*Euspongia*).
„ 3. Monactinellidæ (*Halichondria*, &c.)
„ 4. Tetractinellidæ (*Geodia*, *Tethya*, &c.)
„ 5. Lithistidæ (*Discodermia*, &c.)
„ 6. Hexactinellidæ (*Holtenia*, &c.)
„ 7. Octactinellidæ (*Astræospongia*).
„ 8. Heteractinellidæ (*Asteractinella*, &c.)

[The last six of the above-mentioned orders are regarded by Hinde as sub-orders, and are included in the single order *Silicispongiæ*.]

Class II. Calcispongiæ.

Family 1. Ascones (*Ascetta*, &c.)
„ 2. Leucones (*Leucandra*, &c.)
„ 3. Sycones (*Grantia*).
„ 4. Pharetrones (*Corynella*, &c.)

Class I. Plethospongiæ.

The Sponges included in this class are occasionally destitute of hard structures, but the great majority possess a skeleton, which may be composed of horny fibres alone, or of siliceous spicules alone, or which is formed by a combination of these two sets of structures. In no case is the skeleton composed of carbonate of lime.

Order 1. Myxospongiæ.—The Sponges of this order are entirely destitute of skeletal structures, or, at most, possess a few scattered siliceous spicules. The type-genus is *Halisarca*, comprising a number of soft fleshy sponges, widely distributed in recent seas, which form crusts upon submarine objects. No example of this order, as might be expected from the soft nature of the organism, is known as occurring in the fossil condition.

Order 2. Ceratospongiæ.—In this group of Sponges, the skeleton is composed of the horny substance known as "spongin," and there are either no proper spicules, or in some cases a few siliceous spicules may be scattered in the mesoderm. The horny fibre of the skeleton forms a close reticulation or network (fig. 48, A), and can be shown to consist of a delicate axial thread of organic matter surrounded by a laminated horny sheath. In many cases, the horny fibre includes numerous sand-grains or other foreign bodies in its interior (fig. 48, B), these being taken in at the free-growing ends of the fibres, to which they form a kind of core, replacing the soft organic axis which in some cases is alone present. The type of this order is the recent genus *Euspongia*, comprising the Turkey Sponges of commerce. No undoubted fossil representatives of the *Ceratospongiæ* have been as yet detected in the fossil condition, the cylindrical antler-shaped bodies from the Cretaceous rocks of Germany, which Geinitz described under the name of *Spongites*, being of an altogether problematical nature.

Order 3. Monactinellidæ.—This order comprises an extensive series of Sponges characterised by the possession of a skeleton which is typically composed of horny fibres with included spicules of flint. The spicules vary much in form, but are always uniaxial, being most commonly fusiform, pin-shaped, or bow-shaped (fig. 49, *a*, *b*, *c*, and fig. 52). In recent Monactinellids the proportion borne by the spicules to the horny fibre is very variable, and in some types the skeleton consists almost wholly of uniaxial spicules without any, or with

very little, horny connecting-substance (fig. 48, D). In addition to the proper skeleton-spicules, which are usually connected by a horny fibre, there are developed in the mesoderm more or less numerous disconnected, uniaxial, siliceous needles or "flesh-spicules."

The order of the *Monactinellidæ* is represented by a very large number of existing marine Sponges, as well as by the fresh-water group of the *Spongillidæ*. Owing to the nature of the hard structures in this order, the entire skeleton does not readily admit of preservation, and most of the known fossil forms are therefore repre-

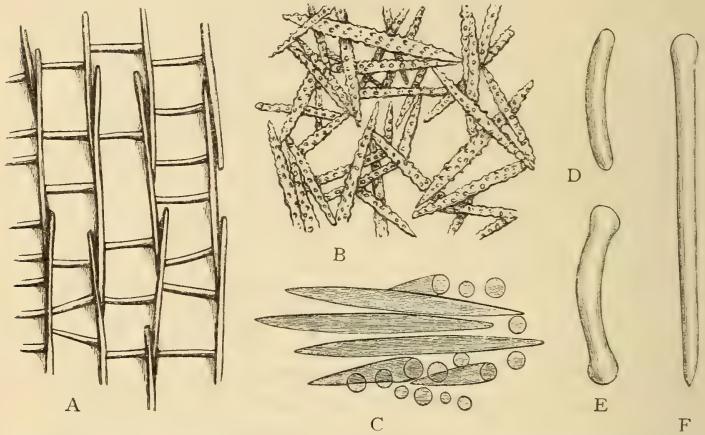


Fig. 52.—Fossil Monactinellid Sponges. A, Part of the spicular network of *Climacospongia radiata*, Silurian, Tennessee, enlarged twelve times; B, Part of the spicular network of *Acanthoraphis intertextus*, Chalk, Kent, enlarged ten times; C, Spicules of *Spongilla Purbeckensis*, as shown in a thin slice of chert from the Purbeck formation, enlarged; D, Spicule of *Reniera gracilis*, Carboniferous, Yorkshire, enlarged sixty times; E, Spicule of *Reniera clavata*, Carboniferous, Yorkshire, enlarged sixty times; F, Spicule of *Axinella paxillus*, Carboniferous, Lancashire, enlarged thirty times. (C is after John Young, and the remaining figures are after Hinde.)

sented by mere fragments or by detached spicules. The record of the distribution of the Monactinellid Sponges in past time is, therefore, necessarily a very imperfect one. The oldest types which have been determined with any certainty occur in the Silurian deposits, in which are found the large uniaxial spicules upon which Hinde has founded the genus *Atractosella*. Of the same age is the genus *Climacospongia* (fig. 52, A), in which the skeleton is composed of elongated acerate spicules arranged in a ladder-like manner. Certain tubular borings in Silurian shells have also been referred to the operations of a Sponge (*Vioa prisca*), supposed to be related to the living boring Sponges (*Cliona*), but the nature of these is very doubtful. On the other hand, fossil shells pierced by borings in all respects similar to those produced by the recent *Clionæ* are not uncommon in Secondary and Tertiary deposits. In the Devonian rocks, Monac-

tinellid Sponges are almost unknown, but strata of this age in Belgium have yielded remains on which the genus *Lasiocladia* has been founded. In the Carboniferous system, on the other hand, particularly in some of the chert-beds associated with the Mountain Limestone and Yoredale series, the remains of Monactinellid Sponges are comparatively abundant. The best known types of this age are *Reniera* and *Axinella*, the former represented by cylindrical spicules (fig. 52, D and E), and the latter by pin-shaped spicules (fig. 52, F). In the genus *Haplistion* more or less complete specimens have been found, showing that the sponge possessed a fibrous skeleton composed of minute, straight, or curved, acerate spicules.

In the Permian rocks no certain remains of Monactinellid Sponges are known, the *Spongillopsis* of Geinitz being apparently inorganic; and the Trias has also yielded so far no traces of this group. In the Jurassic system also, vast as is the number of known Sponges belonging to other orders, no type of the Monactinellids has hitherto been recognised till the very summit of the formation is reached. In the Purbeck beds, however, in chert containing the remains of the fresh-water *Chara*, are found numerous spicules belonging to a fresh-water Sponge, to which the name of *Spongilla Purbeckensis* has been given (fig. 52, C). In the Cretaceous system, likewise, the remains of Monactinellids are very rare, but the Upper Chalk has yielded shells bored by species of *Cliona*, and also the skeleton of the genus *Acanthoraphis* (fig. 52, B), in which the spicules are fusiform and minutely tuberculate. In the Tertiary rocks, lastly, the Monactinellids are mostly, if not wholly, represented by the tunnels bored in shells by species of *Cliona*.

Order 4. Tetractinellidæ.—This order comprises marine Sponges in which the skeleton consists of siliceous skeleton-spicules, frequently arranged in bundles in a radiating manner, and held together by spongin. The characteristic skeleton-spicules are tetraxial, the commonest form being that of an elongated rod carrying three shorter summit-rays at the upper end (fig. 49, *d*). In addition to the typical tetraxial spicules there are usually other uniaxial forms, as well as smaller "flesh-spicules," generally of a globate, stellate, or reniform shape.

The Tetractinellid Sponges are largely represented at the present day, the genera *Tethya* and *Geodia* being well-known examples of the group. Owing to the want of a continuous siliceous skeleton, however, the Tetractinellids are not commonly preserved as fossils, and they are usually represented by detached spicules only. The oldest known examples of this order occur in the Carboniferous rocks, which have yielded the remains upon which the genera *Geodites* and *Pachastrella* have been founded. The former of these is supposed to be allied to the recent *Geodia*, and is characterised

by the possession of elongated spicules with bifid or trifid summits, associated with a dermal layer of globate or reniform spicules. The genus *Pachastrella*, again, comprises "massive, nodose, platter-shaped, or irregularly expanded Sponges without a specialised dermal layer" (Hinde). The skeleton is composed of four-rayed spicules, associated with acerate spicules. The oldest species of *Pachastrella* are found in the Carboniferous, but other forms of the genus have been recognised in the Jurassic rocks, the Upper Chalk, and the Eocene Tertiary. In the Upper Chalk occur the remains of various Tetractinellid Sponges, of which the genus *Tethyopsis* is perhaps the most characteristic. In this genus (fig. 53), the skeleton is composed of radiately arranged trifid spicules, mingled with acerates, while the surface is covered with a layer of minute trifid anchorate spicules (Zittel).

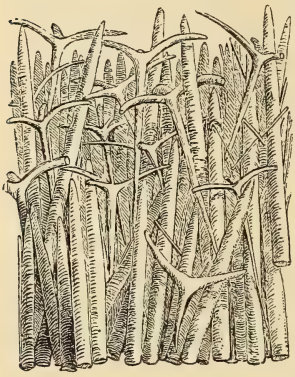


Fig. 53.—Part of the skeleton of *Tethyopsis Steinmanni*, from the Upper Chalk. Enlarged 14 times. (After Zittel.)

Order 5. Lithistidæ. — The Sponges included in this order are massive, stony, and thick-walled, with a very variable external figure. The skeleton is composed principally of four-rayed or irregular spicules (fig. 54), which usually branch at their extremities, their ends being blunt, or being furnished with minute articular surfaces. The skeletal spicules are not fused together, but are so interlocked "by the intertwining of their branches or by the close apposition of their expanded extremities" (Hinde) as to give rise to a practically continuous framework (fig. 54, B). There are generally small monaxial "flesh-spicules," and also a dermal layer of trifid or discoid spicules, in addition to the ordinary skeleton-spicules. There may be a single terminal osculum only, or the Sponge may be provided with numerous scattered oscula; while the canal-system exhibits numerous modifications in different groups of the order, and in some cases is not developed as a special structure.

The order of the Lithistid Sponges has been divided by Zittel into the four following sub-orders :—

1. *Rhizomorina.*—In this group of Lithistids the skeleton-spicules are elongated and irregularly branched (fig. 55, B), the branches terminating in minute articular surfaces which unite adjoining spicules into an irregular and confused network. Typical genera are *Cnemidiastrum*, *Seliscothon* and *Verruculina*.

2. *Megamorina.*—In this group the skeleton-spicules are large and either simple or irregularly branched, the branches terminating in obtuse

ends or expanded articular surfaces. The spicules form an open meshwork by the apposition of their terminal facets. Typical genera are *Doryderma*, *Pachypoterion*, and *Carterella*.

3. *Anomocladina.*—In this group the skeleton-spicules have the form of a central node from which radiate simple or bifurcate arms, which have slightly expanded ends, and are variable in number. The skeleton forms a regular network produced by the union of the expanded ends of the spicular arms with the nodes, or sometimes with the branches of adjoining spicules (fig. 55, A). Typical genera are *Vetulina*, *Hindia*, and *Astylospongia*.

4. *Tetracladina.*—In this group, the spicules (fig. 54) consist of four rays which meet in a non-inflated centre in such a way that one ray

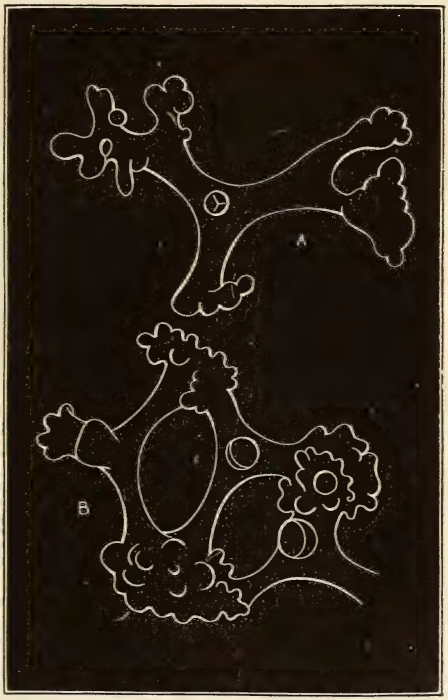


Fig. 54.—A, A single skeleton-spicule of the living Lithistid *Discodermia polydiscus*, magnified 60 diameters; B, Small portion of the skeleton of *Siphonia pyriformis*, similarly enlarged. (After Sollas.)

forms a shaft from which the other three rays spring, approximately meeting at angles of 120°. The ends of the rays are branched, and interlock with the ends of adjoining spicules to form a continuous meshwork. Typical examples are the genera *Jerea* (fig. 49, *e*), *Aulocopium*, and *Siphonia* (fig. 58).

The Lithistid Sponges are all inhabitants of the sea, and the existing genera (*Discodermia*, *Corallistes*, *Vetulina*, &c.) are mostly

found in water of moderate depth. As regards the distribution of the order in time, one of the most ancient representatives of the group would appear, from the researches of Dr Hinde, to be the genus *Archæoscyphia* (based upon the *Archæocyathus Minganensis* of Billings), which occurs in the Upper Cambrian rocks (Calciferous series) of Canada, along with allied types such as *Calathium*. Closely related forms are found at a corresponding geological horizon (the Durness Limestone) in Britain. The skeleton in *Archæoscyphia Minganensis* (fig. 56) has the form of a curved funnel attached by its pointed base, and with a deep central cavity or "cloaca" apparently without an internal wall. The constituents of the skeleton have a radial disposition, and distinct spicules, usually four-armed, and inter-

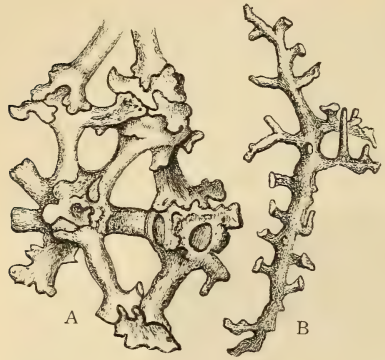


Fig. 55.—A, Part of the spicular network of *Astylospongia*, from the Silurian of Gotland, enlarged 60 times; B, Rhizomorine spicule of *Seliscothon Mantelli*, from the Cretaceous rocks, enlarged 60 times. (After Hinde.)

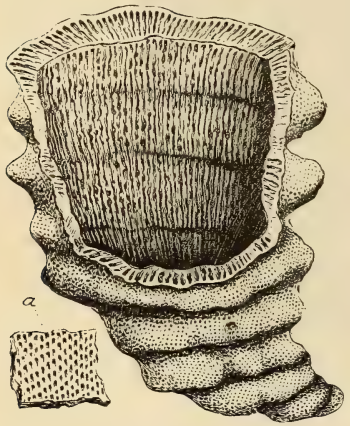


Fig. 56.—Restoration of the lower part of *Archæoscyphia Minganensis*. *a*, The pores of the inner wall of the cup. Ordovician. (After Billings.)

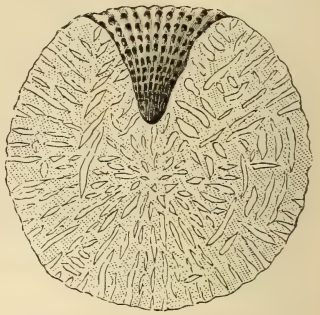


Fig. 57.—Section of *Astylospongia præmorsa*, Silurian, Tennessee. (After Roemer.)

linked by their subdivided ends, are present. The siliceous nature and spicular structure of the skeleton in *Archæoscyphia Minganensis* render it clear that we have to deal here with a genuine Sponge.

In the Ordovician rocks we meet with species of the genera *Hindia* and *Astylospongia*, both of which are represented, still more abundantly in Silurian strata. The genus *Astylospongia* (fig. 57) comprises globular or ovate, unattached sponges, furnished with a cup-shaped or funnel-shaped depression at the summit. There are two principal sets of aquiferous canals, those of the one series being radial and directed from the surface towards the centre, while those of the other series are radial, but are vertically disposed in a direction parallel to the surface, so as ultimately to open into the summit-cup. *Astylospongia* was formerly referred to the Hexactinellids, but recent researches have shown that it is truly referable to the Anomocladine group of the Lithistids. The skeleton consists of siliceous spicules (fig. 55, A) with solid nodes, from which radiate from six to nine straight rays, the ends of which are branched and are furnished with slightly expanded articular processes. The rigid skeletal network is formed by the apposition of the branched ends of the spicules to the nodes of adjoining spicules, or, sometimes, to the ends of their immediate neighbours. More or less closely allied to *Astylospongia* are the Silurian genera *Palæomanon* and *Protachilleum*, and probably the Ordovician genus *Eospongia*; while the Jurassic genera *Melonella* and *Cylindrophyma*, the Cretaceous *Mastosia*, and the recent *Vetulina* are regarded by Zittel as belonging to the same family.

The genus *Hindia* comprises free, spherical or subspherical sponges, in which the body is traversed by numerous canals which radiate from a central space and open on the surface. The skeleton consists of four-rayed spicules, the digitated ends of which embrace the nodes or rays of adjoining spicules in such a way as to form a regular meshwork. The species of the genus are chiefly found in the Ordovician and Silurian rocks, but spicules have been recognised by Hinde in strata of Carboniferous age.

No Devonian Lithistids are at present known, but a few forms of this group (*Cnemidiastrum* and *Doryderma*) have been recognised in the Carboniferous deposits. No forms of the *Lithistidæ* are known in the Permian or Triassic rocks, but very numerous types of this order of sponges have been recognised as occurring in the Jurassic deposits. In the Upper Jurassic rocks of Germany, in particular, are numerous Lithistids, belonging to such genera as *Cnemidiastrum*, *Hyalotragos*, *Platychonia*, *Placonella*, &c. It is, however, in the upper portion of the Cretaceous system that the Lithistid Sponges attain their maximum development, the genera *Chenendopora*, *Siphonia*, *Verruculina*, *Chonella*, *Jerea*, *Jereica*, *Bolidium*, *Turonia*, *Plinthosella*, &c., being characteristic and widely distributed types. Of all the Cretaceous Lithistids none is more generally familiar than the genus *Siphonia* (fig. 58), in which the sponge consists of a pyriform or subspherical body, supported

usually on a longer or shorter stem, and attached thereby to some foreign body. In some cases, however, the stem is wanting, and the sponge is attached simply by diverging root-fibres. The exhalant water-canals open at the summit of the sponge by oscula situated within an apical cavity or cloaca, while the inhalant canals open by pores on the lateral surfaces. The skeleton-spicules (fig. 54, B) are four-armed, the ends of the rays being expanded and furnished with tubercles and intervening depressions, by means of which they are interlocked with the rays of adjoining spicules so as to produce a rigid framework. As pointed out by Sollas, there is a close agreement in form between the spicules of *Siphonia* and those of the recent genus *Discodermia*. The genus *Jerea* is very closely allied to *Siphonia*, but there is no general cloacal chamber; while in the related genus *Hallirhoa* the body of the sponge is lobed.

Fig. 58.—*Siphonia ficus*, a Cretaceous Lithistid Sponge.

In the Tertiary period, lastly, the remains of Lithistids are for the most part of infrequent occurrence, though numerous sponges belonging to this order have been detected in Miocene strata in Algeria.

Order 6. Hexactinellidæ.—In this group of the siliceous Sponges, the skeleton is composed of six-armed flinty spicules, the rays of which are at right angles to each other (fig. 59, B). In the centre of each spicule are three canals cutting each other at right angles, and forming an axial six-rayed tube. In some Hexactinellid Sponges, the spicules are simply united by the soft tissues. More commonly, the spicules are fused with one another by the ends of corresponding rays, or are united by means of amorphous silica, so as to form a trellis-work of rectangular or polyhedral meshes, the individual spicules of which may be only recognisable by the persistence of their axial canals (fig. 63). The "flesh-spicules" are fundamentally six-armed, but may give off secondary branches so as to form a rosette.

The Hexactinellid Sponges may be divided into two groups according as the skeletal spicules are fused with one another or are free. In the group of the *Dictyonina*, comprising such genera as *Euplectella*, *Ventriculites*, *Tremadictyon*, *Cœloptychium* (fig. 59), and many others, the skeleton is composed of six-armed spicules which became fused with one another by a secondary deposit of silica, so as to form a latticed trellis-work. On the other hand, in the group of the *Lyssakina*, comprising such genera as *Stauractinella* and *Hyalostelia*, the skeletal spicules are interlaced, and are usually

simply held in position by the soft parts of the sponge, no fusion taking place between them.

The recent Hexactinellids are all inhabitants of the sea, and are mostly found in deep water, and palæontologists are now acquainted with a very extensive series of fossil forms, dating from the Cam-

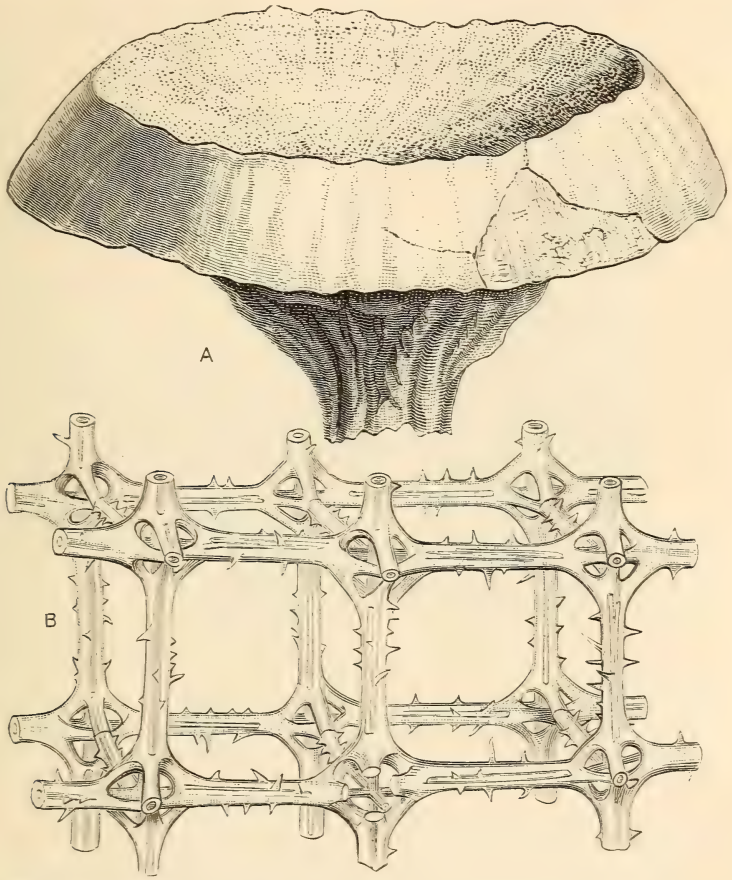
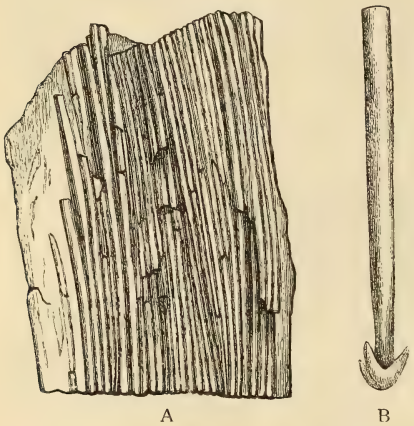


Fig. 59.—A, Side-view of a specimen of *Cæloptychium Seebachi*, of the natural size, from the Cretaceous formation; B, Portion of the hexradiate skeleton of the same, enlarged 65 times. (After Zittel.)

brian period. The oldest known type of the *Hexactinellidæ* is the genus *Protospongia*, species of which occur in deposits of Cambrian age. In this genus, the sponge is cup-shaped, with a thin wall, composed of large cruciform spicules arranged so as to form a quadrate network, the interspaces of which are filled up by similarly dis-

posed cross-shaped spicules of smaller size (fig. 50). Owing to the condition of preservation of the sponge, it is still not absolutely certain whether the spicules were fused with one another or free, but it would seem probable that the former was the case, and that the genus belongs therefore to the Dictyonine section of the Hexactinellids.

Another very ancient genus of this order is *Hyalostelia*, one of the Lyssakine section of the Hexactinellids, which is first known in the Cambrian deposits, is found in Ordovician and Silurian strata, and is abundantly represented in the Carboniferous rocks. Detached spicules from the Chalk have also been referred here. The genus *Hyalostelia* is related to the recent genus *Hyalonema*, comprising the so-called "Glass-rope Sponges." The body of the Sponge in *Hyalostelia* is imperfectly known, but is composed of siliceous spicules some of which are of the hexactinellid type, with one ray much elongated, while others are variously modified. The sponge was attached to the sea-bottom by a long "rope" of cylindrical or rod-like, siliceous "anchoring spicules," which often terminate at their distal ends in four recurved rays (fig. 60). The "rope" is the part usually found in the fossil condition, and in the case of the *Hyalostelia parallela* of the Carboniferous rocks it was originally described as a tubicolar Annelide, under the name of *Serpula parallela*.



A B

Fig. 60.—A, Part of the anchoring-rope of *Hyalostelia Smithii*, from the Carboniferous Limestone, of the natural size; B, Fragment of one of the anchoring spicular rods of the same species, showing four recurved rays at the distal end, enlarged ten diameters. (After Hinde.)

In strata of Ordovician age, the Hexactinellid Sponges are represented not only by the genus *Hyalostelia*, but also by the singular group of the *Receptaculitidæ*, the true relations of which have been recently determined by Dr George J. Hinde. The two principal genera of this family—viz., *Receptaculites* and *Ischadites*—have long been known to palæontologists, but the investigation of their structure has proved to be attended with great difficulties, and various opinions have been held as to their relations and systematic position. In *Receptaculites* (fig. 61) the organism is a cup-shaped or platter-shaped body which grows from a small inversely conical

nucleus, and may reach a foot or more in diameter, but is not attached by a stem to the sea-bottom. In the nearly allied *Ischadites*, the organism is conical, ovate, or pyriform in shape, with a summit-aperture leading into a central cavity. In *Receptaculites*, on the other hand, there is no distinct evidence that the cup-shaped cavity was ever roofed over as it is in *Ischadites*. The internal

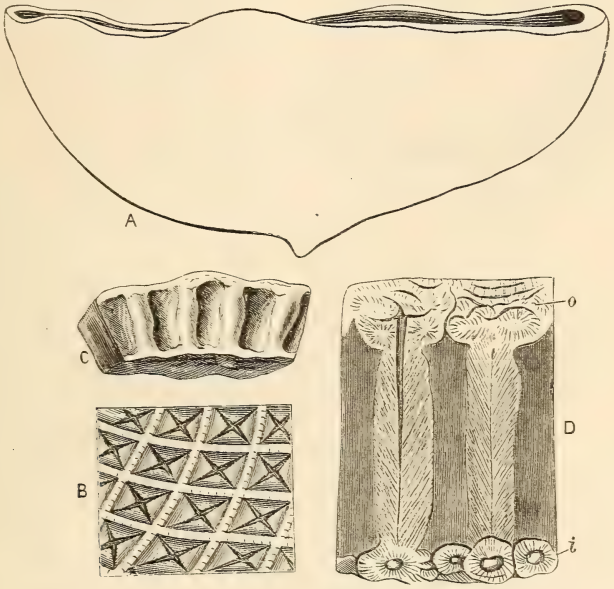


Fig. 61.—Morphology of *Receptaculites*. A, Outline of a perfect, basin-shaped specimen of *Receptaculites Neptuni*, viewed in profile, of the natural size; B, Part of the outer integument of the same, enlarged two diameters, and so far weathered as to show the four transverse or horizontal rays which underlie the summit-plates of the skeleton-spicules; C, Side-view of a fragment of the same, showing the skeletal spicules; D, Vertical section of the same, magnified, showing the skeletal spicules with their axial canals and expanded extremities. From the Devonian of Germany. (After Gümbel.)

structure of these singular organisms will be best understood by reference to fig. 62, which is an ideal figure constructed by Mr Billings to show the morphological characters of *Receptaculites*. It should be noted, however, that this figure, though well representing the *structure* of *Receptaculites*, gives an incorrect idea of the *form* of the organism; since the known species of this genus are cup-shaped and open superiorly, as shown in fig. 60, A. The cup-shaped body of *Receptaculites* is furnished with a thick wall composed of pillar-like spicules arranged at right angles to the surface. These spicules are shown in thin sections (fig. 61, D) to be furnished in their interior with an axial canal, and they are expanded at their outer ends

into rhomboidal "summit plates" (fig. 61, B), which fit into one another so as to form a mosaic-like outer layer or membrane, the plates being disposed in decussating lines. Immediately below, or internal to, the summit-plates, the vertical spicules give off four transverse or horizontal rays, which only become visible externally when the surface-plates are worn away or are viewed from the inside (fig. 61, B). At their inner ends, where they abut upon the central cavity of the organism, the vertical spicules expand so as to form small horizontal plates (fig. 62, *b*), which are traversed by horizontal canals, and are so apposed to each other as to give rise to an inner calcareous membrane. In one species of the genus, if not in all, the plates of this inner membrane are so disposed as to leave cylindrical canals at their angles of junction, through which the water which has filtered between the summit-plates of the outer layer of plates is admitted to the internal cavity of the organism. In most specimens of *Receptaculites* the skeleton-spicules are now composed of calcite or peroxide of iron, but Hinde has adduced evidence to show that the spicules were originally siliceous, and that their present condition is the result of replacement. The species of *Receptaculites* are widely distributed in the Ordovician and Silurian deposits, and are also well represented in the Devonian rocks, while a species is recorded as occurring in the strata of Carboniferous age.

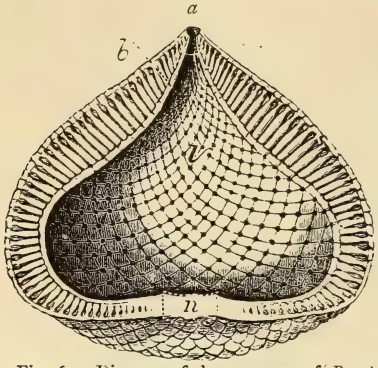


Fig. 62.—Diagram of the structure of *Receptaculites*, as it would be shown by a vertical section of a perfect specimen. *a*, The aperture at the summit; *b*, The inner plates of the spicules; *c*, The summit-plates of the spicules; *n*, The usual position of the nucleus; *v*, The great internal cavity. The unshaded bands running from the outer to the inner integument represent the spicules. (After Billings.) The *form* of this figure agrees with that of *Ischadites*, the body in *Receptaculites* being of the nature of an open cup or bowl.

The genus *Ischadites*[1] comprises fossils which are in many respects closely allied to *Receptaculites*, but in which the central cavity is roofed over superiorly, instead of being widely open as it is in the latter genus. The *form* of the organism is, therefore, that represented in the diagrammatic figure of *Receptaculites* given above (fig. 62), being conical or pyriform, usually with a summit-perforation opening into the central cavity. The wall of the organism is composed of cylindrical, pillar-like spicules, arranged at right angles to the surface, and in most respects similar to the corresponding structures in *Receptaculites*. The outer ends of these hexactinellid spicules are modified to form rhomboidal

[1] The fossils to which the name *Tetragonis* have been given belong in part to *Ischadites*, and are in part referable to the Hexactinellid genus *Dictyophyton*.

"summit-plates," which are nearly in contact, and are arranged in obliquely curved intersecting rows, giving the external surface of the fossil very much the appearance of the engine-turned case of a watch. Internal to the summit-plate, each radial spicule gives off four transverse or horizontal rays, as in the genus *Receptaculites;* but the inner ends of the radial spicules simply terminate in pointed extremities, and there is, therefore, no internal plated membrane such as characterises the latter genus. The species of *Ischadites* are found in the Ordovician rocks, and, more abundantly, in Silurian deposits, but they are not known to have survived into the Devonian period. Nearly allied to *Ischadites* is the genus *Acanthochonia*, which is also of Silurian age. Lastly, the genus *Sphærospongia* includes pyriform or cup-shaped organisms, the outer integument of which consists of regularly arranged hexagonal calcareous plates, which represent the expanded outer ends (or "summit-plates") of a series of Hexactinellid spicules. Immediately below, or internal to, the summit-plate, each spicule gives off four transverse or horizontal rays, but the actual stem of the spicule, or, in other words, its radial ray, is either aborted or is represented only by a short knob-like projection. The species of *Sphærospongia* are confined, so far as known, to the Devonian rocks.

In spite of their abnormal form and structure, as compared with recent types, there seems to be no reason for doubting that Dr Hinde is correct in his view that the genera *Receptaculites*, *Ischadites*, *Acanthochonia*, and *Sphærospongia* constitute a peculiar group of Lyssakine Hexactinellid Sponges, all the members of which are Palæozoic.

In rocks of Silurian age, the Hexactinellid Sponges are represented not only by the Anchoring-Sponges belonging to the genus *Hyalostelia* and by the abnormal genera of the *Receptaculitidæ* just noticed, but also by the curious types known as *Dictyophyton* and *Plectoderma*. The genus *Dictyophyton* comprises cylindrical or cup-shaped sponges, apparently not attached to foreign bodies, in which the wall consists of a connected spicular framework disposed so as to form a series of quadrangular areas. The precise structure of the spicules and their mode of union are points as yet imperfectly known. The species of *Dictyophyton* are not only found in the Silurian rocks, but likewise in Devonian strata, and species occur also in the Carboniferous deposits. The Silurian genus *Plectoderma* is related to *Dictyophyton*, but the spicular network is much less regular.

In the Devonian deposits, the groups of Hexactinellids represented by *Sphærospongia* and *Dictyophyton* still persist, but our knowledge of other types is very imperfect. In the Carboniferous period, again, the Hexactinellids are chiefly represented by the genus *Hyalostelia*, the anchoring fibres of which are not very uncommon in the lower beds of the system; but other genera of the *Lyssakina* (such as *Holasterella*) are likewise represented.

In the Permian and Triassic systems, so far as our certain knowledge goes, Hexactinellid Sponges may be said to be still unknown; though the imperfectly examined *Bothroconis* of King, from the Permian of the North of England, may possibly belong here.

On the other hand, in the Jurassic rocks the Hexactinellid Sponges, though comparatively few in number in the lower division of the system, attain a great development in the upper beds of the system, in certain regions. Of the Jurassic Hexactinellids, *Craticularia*, *Verrucocœlia*, *Tremadictyon* (fig. 63), *Sporadopyle*, and *Sphenaulax* possess a skeleton built upon the same type as the recent *Eurete* and *Farrea ; Pachyteichisma* and *Trochobolus* are early forms of the great

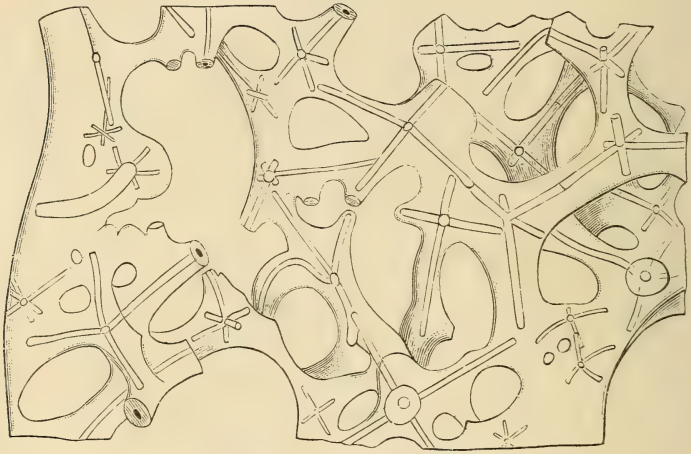


Fig. 63.—Portion of the skeleton of *Tremadictyon reticulatum*, enlarged 50 diameters, from the Jurassic rocks. (After Zittel.) The original spicules are soldered into a continuous trellis-work by a coating of silica ; but their position and hexradiate form is shown by their axial canals. The "crossing-nodes," or points of intersection of the arms of each spicule, are solid.

family of the *Ventriculitidæ ; Cypellia*, *Stauroderma*, and others represent the extinct family of the *Staurodermidæ ;* and *Stauractinella* belongs to the group of Hexactinellids (*Lyssakina*) in which the skeleton-spicules are only united by sarcode, so that they do not form a continuous network.

In the Cretaceous deposits, and especially in the Chalk itself, the Hexactinellids are very largely and abundantly represented. Of the family of the *Euretidæ*, with their regular spicular mesh and simple spicular nodes, we have now few forms (*Craticularia*, *Verrucocœlia*, &c.) ; but the great family of the *Ventriculitidæ* and the groups allied to this now undergo a marvellous expansion. In the *Ventriculitidæ* proper, the sponge-body is of variable shape, but usually more or less cup-shaped or infundibuliform (figs. 64 and 65), or cylindrical, the wall being often folded. The skeleton-spicules are always united into a continuous lattice-work, and their "crossing-nodes" are not solid. On the other hand, the point of intersection of the arms of each hexradiate spicule forms an open octahedron, in the centre of

which the central canals of the six rays form a delicate axial cross. The boundaries of the central space are formed by twelve oblique uniting beams, the whole forming an elegant octahedron, which is known as the "lantern" (see the same type of spicule in *Cœloptychium*, fig. 59, B). The sponge-body in the *Ventriculitidæ* was attached to the sea-bottom by a root of fasciculate flinty fibres, and a dermal layer in the form of a cribriform siliceous membrane was

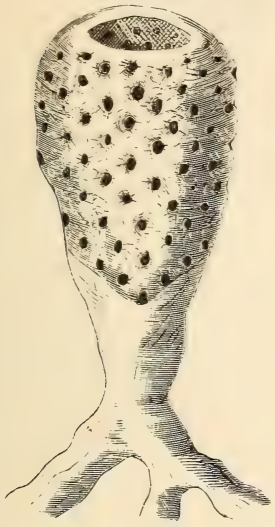


Fig. 64.—*Ventriculites sp.* White Chalk, Britain.

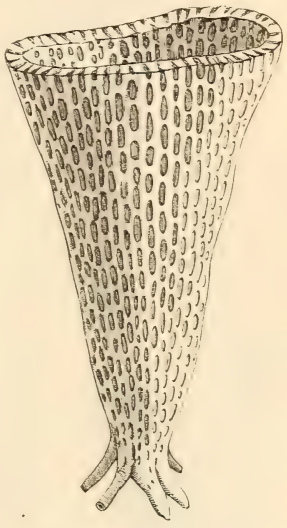


Fig. 65.—*Ventriculites striatus*, from the Cretaceous rocks of Hanover, one-half of the natural size.

present. Typical Cretaceous genera of the *Ventriculitidæ* are *Ventriculites* itself (figs. 64 and 65), of which numerous species are known, *Rhizopoterion* and *Cephalites*.

Closely allied to the preceding is the family of the *Cœloptychidæ*, comprising the beautiful Chalk Sponges which constitute the genus *Cœloptychium* (fig. 59). These are in most respects very similar to *Ventriculites*, but have a flattened or discoid body supported on a short stem, the skeleton being folded into laminated walls which divide the central cavity into radial chambers.

The group of the *Mæandrospongidæ* is also closely related to that of the *Ventriculitidæ*, and comprises variably shaped sponges with folded walls, the folds often anastomosing so as to give rise to open tubes. The genera of this family—such as *Plocoscyphia*, *Tremabolites*, *Etheridgia*, *Toulminia*, and *Camerospongia* (fig. 66)—are mostly Cretaceous, though a few types occur in the Jurassic deposits.

As regards the remaining groups of the Cretaceous Hexactinellids, the body-wall in the family *Callodictyonidæ* is composed of hexactinellid spicules the nodes of which are octahedral, and which give rise by their union to an exceedingly regular open meshwork, while the canal-system is wanting or rudimentary. The Cretaceous genera

Fig. 66.—*Camerospongia fungiformis.* Cretaceous.

Callodictyon and *Pleurope* are good representatives of this family. In the *Mellitionidæ*, are included Sponges in which the walls are closely perforated by tubular canals like the cells of honeycomb, and the spicules have simple nodes. This family includes the Cretaceous genus *Stauronema* and the genus *Aphrocallistes*, which ranges from the Chalk to the present day. The family of the *Coscinoporidæ* comprises variously shaped Sponges, with a close and irregular skeletal network, and having numerous straight, blind, radiate canals which open alternately on both sides of the sponge-wall. In *Coscinopora* itself (fig. 67), the cup-shaped sponge-body is affixed to some foreign object by ramified roots. The lattice-work of the skeleton is irregular, and the crossing-nodes of the spicules are partly solid and partly furnished with a "lantern." In the nearly allied *Guettardia*, which is also Cretaceous in its range, the wall is deeply folded in a stellate manner, and the crossing-nodes of the spicules are solid. Nearly related to the preceding is the family of the *Staurodermidæ*, which, though principally Jurassic in its range, is not without Cretaceous representatives (such as *Eubrochus*).

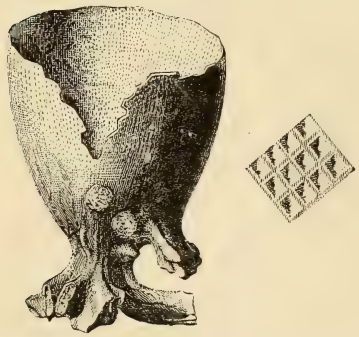


Fig. 67.—*Coscinopora cupuliformis*, and a portion of its surface enlarged. Cretaceous.

The Tertiary Hexactinellids, finally, are comparatively few in number and are imperfectly known, but the order is represented at the present day by such genera as *Euplectella*, *Hyalonema*, *Aphrocallistes*, *Holtenia*, *Eurete*, *Farrea*, and many others.

Before leaving the Hexactinellid Sponges, a few words may be added with regard to the Silurian genus *Amphispongia*, the char-

acters of which are in some respects anomalous. In this curious genus (fig. 68, *c* and *d*) the sponge-body is elliptical, greatly compressed, and free, without any traces of a canal-system. The basal

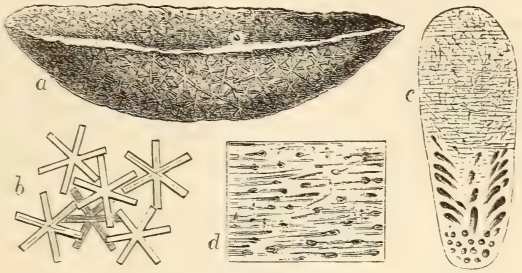


Fig. 68.—*a*, Side-view of a specimen of *Astræospongia meniscus*, of the natural size, Silurian; *b*, Spicules of the same, enlarged (after Roemer); *c*, A split specimen of *Amphispongia oblonga*, of the natural size, Silurian; *d*, Part of the upper portion of the same, enlarged. (Original.)

portion of the sponge consists of large conical spicules, arranged with their pointed lower ends converging towards the middle line; while the upper portion consists of "slender four- and five-rayed spicules with the rays at right angles to each other" (Hinde). The spicules are not fused with one another, and their arrangement is peculiar. In spite of its aberrant character, however, it would seem that *Amphispongia* should be regarded as belonging to the *Hexactinellidæ*.

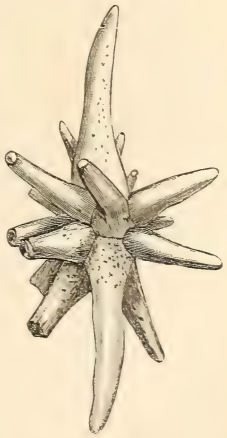


Fig. 69.—Skeleton-spicule of *Asteractinella expansa*, one of the Heteractinellid Sponges, from the Carboniferous rocks, enlarged ten diameters. (After Hinde.)

Order 7. Octactinellidæ.—This order is represented only by the single genus *Astræospongia*, and is characterised by the presence of skeleton-spicules which are normally eight-rayed, six of the rays radiating at equal angles from a central point (fig. 68, *b*), while the other two rays form a vertical axis. The spicules are not fused with one another, and the vertical rays are often obsolete or wholly wanting. The sponges which constitute the genus *Astræospongia* (fig. 68, *a*) are discoid or basin-shaped in form, without any stem of attachment, and without any definite canal-system. The spicules have the form above described, and are now usually found in the condition of calcite. According to the views of Dr Hinde, however, the present calcareous condition of the spicules is the result of secondary changes or replacement, and the skeleton was originally

siliceous. The oldest known species of *Astræospongia* appear in the Silurian, but the genus is principally characteristic of the Devonian system.

Order 8. Heteractinellidæ.—This group has been founded by Hinde to include certain Palæozoic siliceous Sponges in which the skeleton-spicules consist of "an indefinite number of rays, varying from six to thirty, radiating from a common centre" (fig. 69). The body-spicules are irregularly disposed and are not fused with one another; but the dermal spicules are interwoven together, and their rays are partially or completely fused with one another. The genera *Tholiasterella* and *Asteractinella* (fig. 69), included by Hinde in this group, are confined to strata of Carboniferous age, and are only known by detached spicules or imperfect fragments.

Class II. Calcispongiæ.

The class of the Calcareous Sponges comprises, as the name implies, all those sponges in which the skeleton is composed of spicules of carbonate of lime. The spicules vary considerably in form, and different forms are often associated in the same sponge. In living Calcisponges the spicules are never fused with one another, nor united by horny fibre, but in the group of fossil Calcisponges described by Zittel under the name of *Pharetrones*, the skeleton is formed by a reticulated calcareous fibre which is "wholly composed of spicules in close approximation to each other, and as closely interwoven together as the strands of a rope" (Hinde). The following are the principal types of spicules found in the calcareous Sponges. (*a*) Simple uniaxial spicules, which may be associated with the other forms of spicules, or, as in *Pharetrospongia*, may be the only forms present. (*b*) Three-rayed spicules, in which all the rays are in one plane and the rays and angles are equal (figs. 70 and 71, B). In some cases the spicules are triradiate, but two of the three rays are paired and equal, and the third ray is longer or shorter than the other two. (*c*) Four-rayed spicules, with three rays equal and in one plane, but with a fourth ray directed at right angles or obliquely to the others.

The recent Calcisponges are all of small size and are inhabitants of comparatively shallow water, all being marine. By Vosmaer the *Calcispongiæ* are divided into the following two orders:—

Order 1. Homocœla.—In this order there are no special "flagellated chambers," and the canal-system can hardly be said to exist in a definite form; but the thin walls of the sponge (fig. 70) are perforated by numerous pores opening directly into a general cavity, which is lined by ciliated epithelium and terminates on the surface by a single osculum. The order corresponds with the

Ascones of Haeckel, and includes the recent genus *Leucosolenia* (=*Ascetta*). No fossil forms belonging to this order are known to occur.

Order 2. Heterocœla.—In this order "flagellated chambers" are present, and there is a canal-system of different form in the different families of the order. In the family of the *Syconidæ* (=the *Sycones* of Haeckel) the flagellated chambers are elongated, and constitute a series of radial tubes which open directly into a central cloacal chamber. This family includes such recent genera as *Grantia* and *Sycon*, together with the Jurassic genus *Protosycon*. This latter is the earliest representative of the modern Calcisponges, and possesses a cylindrical or clavate body, with a long tubular cloaca, and having the three-rayed or four-rayed spicules so disposed as to form a series of radial canals.

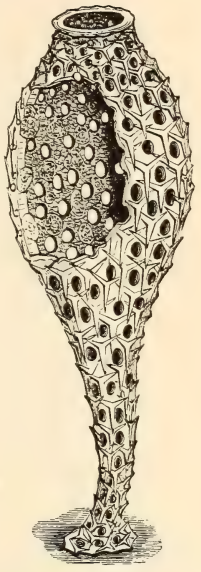


Fig. 70.—*Ascetta primordialis*, a simple Calcareous Sponge, enlarged fifty times. (After Haeckel.)

In the family of the *Leuconidæ* (=the *Leucones* of Haeckel) the flagellated chambers are mostly rounded, and are placed in communication with the cloacal chamber by exhalant canals; while the skeletal spicules are arranged in no definite order. This family includes such recent genera as *Leuconia* and *Leucandra*, detached spicules of both of which have been recognised in the Pliocene beds of St Erth, Cornwall. Very closely allied to this family is the group of the *Teichonidæ*, of which no fossil forms are known.

Lastly, we have the large and important group of the *Pharetronidæ* (the *Pharetrones* of Zittel), all the members of which are extinct. This group includes the largest and most massive of all the Calcisponges, and its characters depart in many important respects from those of all recent forms. The Sponges included by Zittel under the name of *Pharetrones* are variably shaped, simple or branched sponges, with thick walls, and attached by their bases to foreign bodies. In some forms (*e.g.*, in *Peronella*) the canal-system is not distinctly developed, but there is usually a special system of irregular, branched water-canals. The skeleton consists of calcareous spicules disposed to form a network of solid anastomosing fibres (fig. 71, D), and there is a well-developed smooth or wrinkled dermal membrane.

The earliest known types of the *Pharetrones* appear in the Devonian rocks, and belong to the genus *Peronella*, which in later

deposits is represented by very numerous forms. In this genus, the sponge is simple or branched, there is no definite canal-system, and the skeleton consists (where its structure can be determined at all) of anastomosing calcareous fibres composed of comparatively large three-rayed and four-rayed spicules surrounded by similar spicules of small size. Little is known of the *Pharetrones* of the Carboniferous and Permian deposits; but the Upper Triassic beds have yielded numerous forms belonging to such genera as *Eudea*, *Verticillites*, *Peronella*, *Corynella*, and *Stellispongia*. In the Jurassic and Cretaceous rocks the remains of *Pharetrones* are often very abundant, and belong to very numerous genera. Of the many

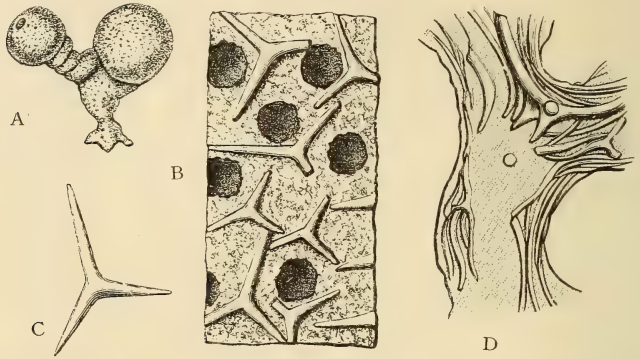


Fig. 71.—*Pharetrones*. A, *Tremacystia D'Orbignyi*, from the Upper Greensand, of the natural size; B, Portion of the outer surface of the same, showing the pores and the spicules of the dermal layer, enlarged thirty times; C, Detached three-rayed spicule, belonging to the dermal layer, enlarged seventy-two times; D, Fragment of the skeleton-fibre of *Elasmostoma scitulum*, showing large three-rayed and four-rayed spicules with small filiform spicules, from the Upper Chalk, enlarged fifty times. (After Hinde.)

Jurassic genera, *Corynella* is perhaps the most important. In this genus we have sponges allied to *Peronella*, but usually possessing a distinct canal-system, and having the reticulated skeleton-fibre composed of "minute, filiform, three-rayed spicules disposed generally parallel with each other in the direction of the fibre" (Hinde). Other largely represented Jurassic genera are *Stellispongia*, *Sestrostomella*, and *Lymnorea*. Of the Cretaceous *Pharetrones*, the genera *Peronella* and *Corynella* still hold a predominant place, but many other types are present, such as *Oculospongia*, *Tremacystia*, *Elasmostoma*, and *Pharetrospongia*. In the genus *Tremacystia* (fig. 71, A) the sponge-body is formed of connected hollow segments, with a common axial tube, and the wall is formed by a single layer of reticulated calcareous fibres penetrated by numerous minute canals. The dermal layer (fig. 71, B and C) is formed of relatively large three-rayed and four-rayed spicules; while the skeleton-fibres are

composed of minute filiform triradiate spicules. In *Elasmostoma* (fig. 71, D) the fibres of the skeleton are composed of large three-rayed and four-rayed spicules, arranged in the centre of the fibre and surrounded by smaller sinuous spicules. Lastly, in the genus *Pharetrospongia*, regarded by Professor Sollas as a Halichondroid Sponge, the skeleton-fibre is composed of minute, straight or slightly curved, uniaxial spicules, arranged parallel with one another in the direction of the fibre.

The latest known representatives of the *Pharetrones* occur in the Maestricht Chalk, but no examples of this group of sponges have been as yet detected in any strata of Tertiary age, nor are any recent forms recognised which could be referred to this remarkable division of Calcisponges.

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CHAPTER XII.

FOSSILS OF DOUBTFUL AFFINITIES.

I. Archæocyathinæ.

The lowest Cambrian strata ("*Olenellus* Beds") of North America, Spain, and Sardinia have yielded the remains of a number of remarkable organisms, which may be collectively spoken of as the *Archæocyathinæ*, but which cannot at present be definitely referred to their place in the zoological series. The three genera which may be regarded as typical of this group of organisms are *Archæocyathus*, *Ethmophyllum*, and *Spirocyathus*, and the characters of these may be briefly treated of here.

There is some difficulty in determining for which of the species described by Mr Billings under the name of *Archæocyathus* this generic title should be retained. If, however, we follow Hinde, and accept *Archæocyathus profundus*, Bill., as the type of the genus, we have to deal with elongated, turbinate, more or less curved fossils, sometimes more than a foot in length, with a diameter of from two to four inches, having a general resemblance to such Rugose Corals as the simple species of *Cyathophyllum*. The conical skeleton is hollow, with a deep, cup-shaped internal cavity, the surface of which shows radiating ridges, and is bounded by a thin inner wall (fig. 72, A). Both the inner and outer walls are perforated by pores, and the space between the two is traversed by numerous vertical septa, which are in turn connected by delicate dissepiments, giving the general structure a vesicular character (fig. 72, B). *Archæocyathus profundus* seems to have been undoubtedly calcareous in its original constitution, and there is no evidence that its skeleton was at any time composed of spicules. The original specimens were obtained in the Cambrian strata of the Straits of Belle Isle, Labrador.

The genus *Ethmophyllum*, as based upon the fossils described by Mr Meek from the Cambrian strata of Nevada under the name of *E.*

Whitneyi, comprises organisms with a general resemblance to *Archæocyathus*. The skeleton in this genus is also superficially very similar to a simple Rugose Coral, being cup-shaped, turbinate, or cylindrical, and either straight or curved (fig. 72 *bis*, A), the external surface being sometimes concentrically annulated or vertically ribbed. There is a deep internal cup (fig. 72 *bis*), the lining of which is perforated by numerous round or oval pores, similar perforations, arranged in vertical and horizontal rows, existing in the outer wall as well. The space between the inner and outer membranes is subdivided by a number (from six to over one hundred) of vertical radiating partitions (fig. 72, B), which have a general resemblance to the "septa" of the Madreporarian Corals. These radiating septa are usually perforated by rounded apertures, which place contiguous interseptal chambers in communication; and they are commonly connected together by irregular transverse plates, resembling the "dissepiments" of many corals. The whole structure of the skeleton is thus more or less porous, and a characteristic feature of the genus is the presence of oblique funnel-shaped canals leading into the internal cup. As in the preceding genus, the skeleton is now calcareous, and microscopic sections show nothing which would prove that its constitution was at any time essentially different, or that definite spicules existed. By Mr Walcott, the fossil described by Mr Billings under the name of *Archæocyathus Minganensis* has been referred to the genus *Ethmophyllum;* but, as previously pointed out, the researches of Dr Hinde have shown that this form was originally siliceous, with a spicular skeleton, and that it is truly referable to the Lithistid Sponges.

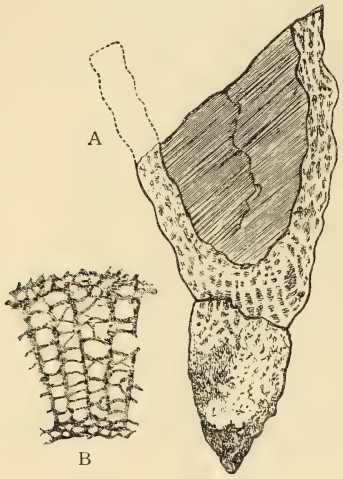

Fig. 72.—A, Longitudinal section of a small specimen of *Archæocyathus profundus*, Bill., slightly reduced in size, showing the reticulated structure of the skeleton and the deep cup at the summit; B, Part of a transverse section of the same, enlarged, showing that the reticulated skeleton has a distinct radial structure, the septa being connected by dissepiments. Cambrian, Labrador. (After Walcott.)

On the other hand, the fossils described by Billings from the Cambrian rocks of Canada under the name of *Archæocyathus atlanticus* would seem to differ considerably in structure from *Archæocyathus* proper (as based upon *A. profundus*, Bill.); and they have recently been referred by Hinde to a new genus under the name of *Spirocyathus* (apparently related to the *Protopharetra* of Bornemann).

The skeleton in *Spirocyathus atlanticus* is conical in form, with a general resemblance to a simple coral, its interior being occupied by a longitudinal tubular cavity (fig. 72 *bis*, C and D). The space between the inner and outer walls is occupied by reticulated calcareous tissue, in which a radial structure is hardly recognisable, while distinct vertical "septa" do not appear to be present. The spaces or irregular canals formed by this calcareous reticulation open on both the outer and inner surfaces of the skeleton by rounded or oval pores. In this case, also, the skeleton seems to have been originally calcareous, and there is no evidence of any spicular structure. *Spirocyathus atlanticus* occurs in the Cambrian rocks of Canada and the United States, and apparently allied types have been discovered by Bornemann in strata of the same age in Sardinia, and have been described by him under the name of *Protopharetra*.

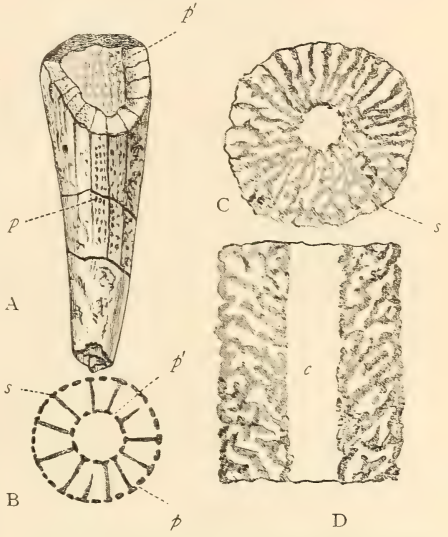

Fig. 72 *bis*.—A, A specimen of *Ethmophyllum Rensselæricum*, Ford, of the natural size; B, Transverse section of the same, showing the outer and inner walls and the radiating septa (*s*); C and D, Transverse and longitudinal sections of *Spirocyathus atlanticus*, Bill. sp. *p*, Pores in the outer wall; *p'*, Pores in the inner wall; *c* The internal cup or chamber. From the Cambrian rocks of North America. (After Walcott.)

The *Archæocyathinæ* are among the most ancient of all known fossils, and are therefore of peculiar zoological interest. It is not, however, possible at present to come to any absolutely certain conclusion as to their systematic position. As their skeleton seems to have been undoubtedly originally calcareous, and as there is no certain evidence (now that the form described by Billings as *Archæocyathus Minganensis* is known to be a Sponge) that their structure was spicular, it would not be possible to refer the group to the *Porifera*. On the other hand, as pointed out by Hinde, the *Archæocyathinæ* show certain unquestionable points of relationship to the Madreporarian Corals. This is particularly seen in the reticulated structure and usually more or less radiate arrangement of the skeletal framework, the skeleton being in many respects comparable with that of such a Perforate Coral as *Calostylis*. At the

same time, the skeleton departs widely in certain of its features (such as the presence of a distinct perforated internal wall) from the Madreporarian type. Upon the whole, therefore, in the present state of our knowledge, it seems best to regard the *Archæocyathinæ* as a group of uncertain affinities, probably more closely allied to the *Madreporaria* than to any other division of the animal kingdom.

II. Pasceolus, Cyclocrinus, and Nidulites.

We may briefly consider here a series of fossils the true affinities of which are at present absolutely uncertain, and which have no particular claim to be taken up in this connection beyond the fact that they have a superficial resemblance to *Receptaculites* and *Ischadites*, and have therefore been commonly placed alongside of these genera. It has, however, been demonstrated by Hinde that the latter are Hexactinellid Sponges, while it seems certain that the fossils here referred to—viz., *Pasceolus* and *Cyclocrinus*—are, at any rate, not referable to the *Porifera*, though their true position is quite problematical.

The genus *Pasceolus* (fig. 73, *a* and *b*) was created by Mr Billings for the reception of some curious Ordovician and Silurian fossils of an ovate or globular form, varying in size from the dimensions of a hazel-nut to those of an apple. The outer layer of the fossil consists of "small convex elevations, composed of a very thin minutely wrinkled layer, which is sometimes translucent" (Hinde). These surface elevations have the general aspect of being hexagonal or pentagonal plates, but there is not sufficient evidence that actual plates are present, and they may be, and probably are, only definitely limited areas of a common calcareous membrane. The inner, concave sides of these polygonal areas are directed *inwards*, towards the central cavity of the fossil (the cup-like plates of *Cyclocrinus* being turned *outwards*); and in well-preserved specimens they exhibit a minutely porous aspect. There is some evidence that the organism was provided with a peduncle of attachment, and in some species a lateral aperture has been described as present. By Mr Billings, it was at first supposed that *Pasceolus* might belong to the *Tunicata*, but this view was subsequently abandoned by him. By later palæontologists the genus has been doubtfully compared with *Receptaculites* or with the *Cystideans*, but its zoological affinities must in the meanwhile be regarded as entirely uncertain.

The genus *Cyclocrinus* was originally founded by Eichwald to include certain ovate or spherical fossils from the Ordovician rocks of Esthonia, which appear to have been free, and which have a thin, plated, external layer enclosing a large central cavity (fig. 73, *e-h*). The outer integument is calcareous, and presents externally the

aspect of being divided into a series of hexagonal or pentagonal areas of very regular form and size (fig. 73, *h*). Each of these areas has the form of a shallow cup-shaped depression, the lower or convex end of which is directed towards the interior of the fossil, and, according to Hinde, is perforated centrally by a small rounded aperture which leads into the central cavity of the organism. According, however, to Ferdinand Roemer, whose figures are here reproduced (fig. 73, *f* and *g*), each of these cup-like plates terminates internally

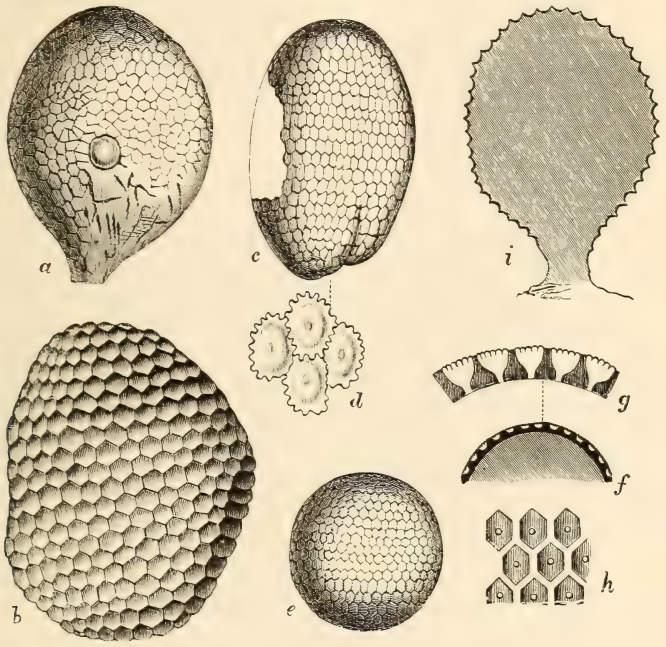

Fig. 73.—*a*, *Pasceolus Halli*, of the natural size (after Billings); *b*, *Pasceolus globosus*, of the natural size (after Billings); *c*, *Pasceolus* (?) *mellifua*, of the natural size (after Salter); *d*, Four of the integumentary plates of the same, enlarged; *e*, *Cyclocrinus Spaskii*, of the natural size (after Ferd. Roemer); *f*, Part of a vertical section of the same; *g*, Part of the last, showing the structure of the integument, enlarged; *h*, Part of the mould of the inner surface, enlarged; *i*, Diagram of a vertical section of *Cyclocrinus* (*Nidulites*) *favus*, showing the form of the body and integumentary plates, and the supposed peduncle (original). All the specimens are from the Silurian, except *b*, which is from the Ordovician.

in a small pillar, and the genus is hence compared by this distinguished palæontologist with *Receptaculites*. Dr Hinde, on the other hand, does not recognise in *Cyclocrinus* any features of resemblance to *Receptaculites*, and considers that the genus is identical with *Nidulites*.

The present writer has not had the opportunity of studying the genus *Cyclocrinus*, and is therefore unable to express a positive

opinion as to its identity with *Nidulites*. It is clear, however, that the two are, at any rate, very closely related, if not absolutely identical. The name *Nidulites* was proposed by Salter for certain singular Silurian fossils (subsequently described by Eichwald under the name of *Mastopora*), which have the form of ovate, globular, or pyriform, hollow bodies, with a thin calcareous external wall, and probably attached to foreign bodies by a peduncle (fig. 73, *i*). The wall of *Nidulites* encloses a large central space, and is formed of short, wide, hexagonal calcareous tubes or cells, which are united together at their basal ends and also by their walls (fig. 74, A and B). The outer ends of these shallow tubes or cells are open, while the inner ends are closed by curved basal plates, the convexities of which are turned towards the central cavity of the organism. Moreover, the closed end of each cell is perforated by a small round central aperture (fig. 74, C), so that each cell communicates freely with the great internal cavity.

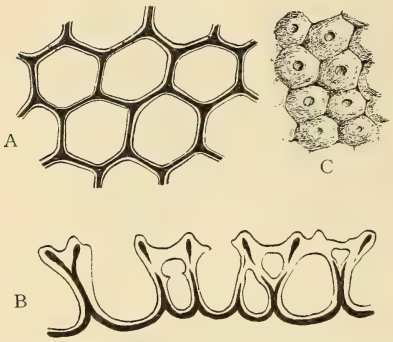

Fig. 74.—Structure of *Nidulites* (=*Mastopora*). A, Tangential section of the wall of *Nidulites*, showing the cup-like plates of the integument transversely divided, so as to give rise to a series of hexagonal cells, enlarged six times; B, Vertical section of the wall of the same, showing the short hexagonal cups or cells of the outer membrane longitudinally divided, similarly enlarged; C, A few of the cup-like plates of the wall, viewed internally and showing the central perforations in their bases, enlarged. From the Silurian rocks of the Island of Oesel. (Original.)

With regard to the affinities and systematic position of *Nidulites* and *Cyclocrinus*, it is not possible at present to give any decided opinion. There is no positive character exhibited by these singular fossils which would enable us to refer them definitely to any known division of the animal kingdom. The resemblances which they present to the *Receptaculitidæ* or to the *Cystideans* are quite superficial, and it is not even clear that they are genuinely related to the equally enigmatical genus *Pasceolus*. It may be pointed out, however, that there are some curious points of resemblance between *Nidulites* and *Cyclocrinus* on the one hand and certain of the Calcareous Algæ (*Siphoneæ verticillatæ*) on the other hand; and it does not seem impossible that these points of resemblance indicate a genuine relationship. If this conjecture should prove to be well founded, these singular fossils may ultimately find a resting-place in the vegetable kingdom.

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5. "Lethæa Palæozoica." 1880. Ferd. Roemer.
6. "On the Structure and Affinities of the Family of the Receptaculitidæ." 'Quart. Journ. Geol. Soc.' 1884. Hinde.

CHAPTER XIII.

SUB-KINGDOM III.—CŒLENTERATA.

GENERAL CHARACTERS AND DIVISIONS OF CŒLENTERATES—HYDROZOA—DIVISIONS OF HYDROZOA.

THE sub-kingdom *Cœlenterata* (Frey and Leuckart) may be considered as a modern representative of the *Radiata* of Cuvier. From the *Radiata*, however, the *Echinodermata* and *Rotifera* have been removed, the entire sub-kingdom of the *Protozoa* has been taken away, and the *Polyzoa* have been relegated to a place near the *Mollusca*. Deducting these groups from the old *Radiata*, the residue, comprising most of the animals commonly known as Polypes or Zoophytes, remains to constitute the modern *Cœlenterata*.

The *Cœlenterata* may be defined as *radially symmetrical animals, in which the mouth opens into a simple or variously divided space ("cœlenteric cavity"), which acts as an alimentary cavity, and which may or may not be divided into two portions, of which one forms a rudimentary digestive tube. The body-wall consists of two fundamental layers ("ectoderm" and "endoderm"), between which an intermediate layer ("mesoderm") is usually developed. Peculiar urticating organs, or "thread-cells," are present. The nervous system is sometimes specialised, sometimes diffused; but no vascular organs are developed. Reproductive organs are invariably present at some period or another of life, though asexual reproduction is also very general.*

The sub-kingdom *Cœlenterata* is divided into the two great primary divisions or classes of the *Hydrozoa* and *Actinozoa*, and the following table indicates the main subdivisions of these:—

TABLE OF THE DIVISIONS OF THE CŒLENTERATA.

CLASS I.—HYDROZOA.

Sub-class 1. HYDROIDA (Hydroid Zoophytes).
a. Hydrida.—Ex. Hydra.
b. Corynida.—Ex. Tubularia, Hydractinia.

c. Thecaphora.—Ex. Sertularia, Campanularia.
d. Trachymedusæ.—Ex. Trachynema.
Sub-class 2. SIPHONOPHORA (Oceanic Hydrozoa).
a. Calycophoridæ.—Ex. Diphyes.
b. Physophoridæ.—Ex. Physalia.
Sub-class 3. LUCERNARIDA (Sea-blubbers).
a. Calycozoa.—Ex. Lucernaria.
b. Acraspeda (*Discophora*).—*Ex.* Aurelia, Rhizostoma.
Sub-class 4. GRAPTOLITOIDEA (Graptolites).
Sub-class 5. HYDROCORALLINÆ (Hydrocorallines).
a. Milleporidæ.—Ex. Millepora.
b. Stylasteridæ.—Ex. Stylaster.
Sub-class 6. STROMATOPOROIDEA (Stromatoporoids).

CLASS II.—ACTINOZOA.

Order 1. ZOANTHARIA.—*Ex.* Sea-Anemones (*Actinidæ*) Corals (*Madreporaria*).
Order 2. ALCYONARIA.—*Ex.* Sea-pens (*Pennatulidæ*), Red Coral (*Corallium*), Organ-pipe Coral (*Tubipora*).
Order 3. CTENOPHORA.—*Ex.* Venus's Girdle (*Cestum*).

As regards their general *distribution in time*, the earliest known remains of Cœlenterates appear in the Upper Cambrian rocks, where the sub-kingdom is represented by ancient types of the *Hydrozoa*.

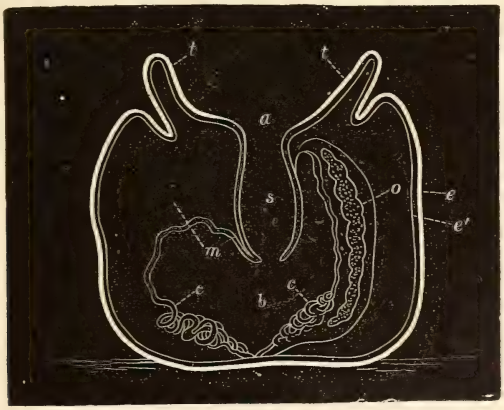

Fig. 75.—Diagrammatic vertical section of a Sea-anemone. *a*, Mouth; *s*, Gullet; *b*, Body-cavity; *c c*, Convoluted cords ("craspeda") forming the free edges of the mesentery (*m*); *t t*, Tentacles; *o*, Reproductive organ contained within the mesentery. The ectoderm (*e*) is indicated by the broad external line, the endoderm (*e'*) by the thin line, and the space between that and the ectoderm represents the mesoderm.

In the Ordovician rocks we find the two great classes of the *Hydrozoa* and the *Actinozoa* thoroughly differentiated, and existing under many and varied types, a fact which would lead us to assign a very high antiquity to the early progenitors of this series

of animals. From the beginning of the Ordovician rocks onwards, the Cœlenterates are very abundant and important as fossils, the large groups of the *Graptolitoidea* and *Stromatoporoidea* being wholly extinct, and having no close relatives now in existence. Owing to the fact, however, that other large groups (such as the Lucernarians, the Oceanic Hydrozoa, and the Ctenophora) are almost or altogether without hard parts, and therefore only capable of preservation in the fossil condition under very exceptional circumstances, the geological history of the sub-kingdom is very imperfect.

Class I.—Hydrozoa.

The class of the *Hydrozoa* comprises those Cœlenterates *in which the walls of the body enclose a simple undivided cavity (the "cœlenteric cavity"), which acts both as a body-cavity and a digestive cavity. An œsophageal tube is not developed; but the upper end of the alimentary*

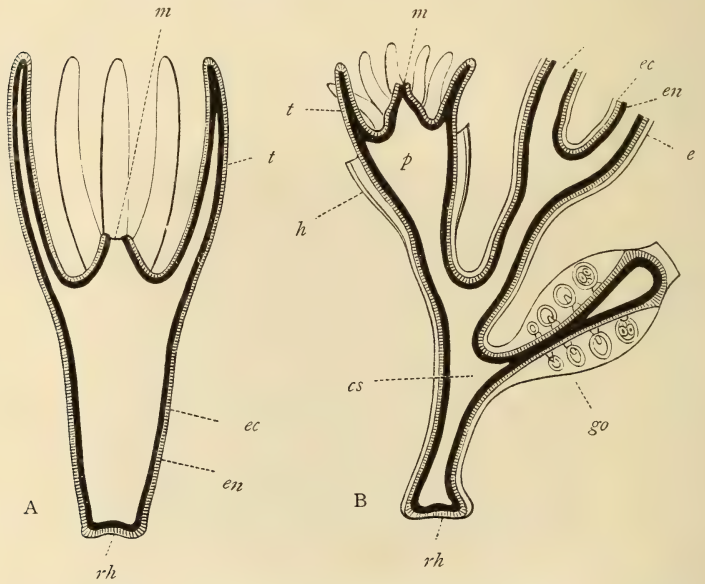

Fig. 76.—A, Diagram of *Hydra*, vertically bisected, and greatly magnified; B, Diagram to show the structure of a compound Hydrozoön (*Sertularia*). *ec*, Ectoderm; *en*, Endoderm; *m*, Mouth, opening into the cœlenteric space or body-cavity; *t*, Tentacle; *p*, Nutritive polypite; *go*, Reproductive bud or "gonophore," consisting of a capsule enclosing a central axis to which reproductive polypites are attached; *cs*, Cœnosarc; *rh*, Hydrorhiza; *pe*, Periderm; *h*, Hydrotheca.

tract may be prolonged into radiating canals united by a peripheral ring. The reproductive organs are external buds, and are often developed in specially modified zoöids (fig. 76).

The simplest type of the *Hydrozoa* is the genus *Hydra*, comprising the Fresh-water Polypes, in which the organism consists of a single tubular or cylindrical "polypite" (fig. 76), furnished at its base or "proximal" extremity with a disc-like sucker or "hydro-

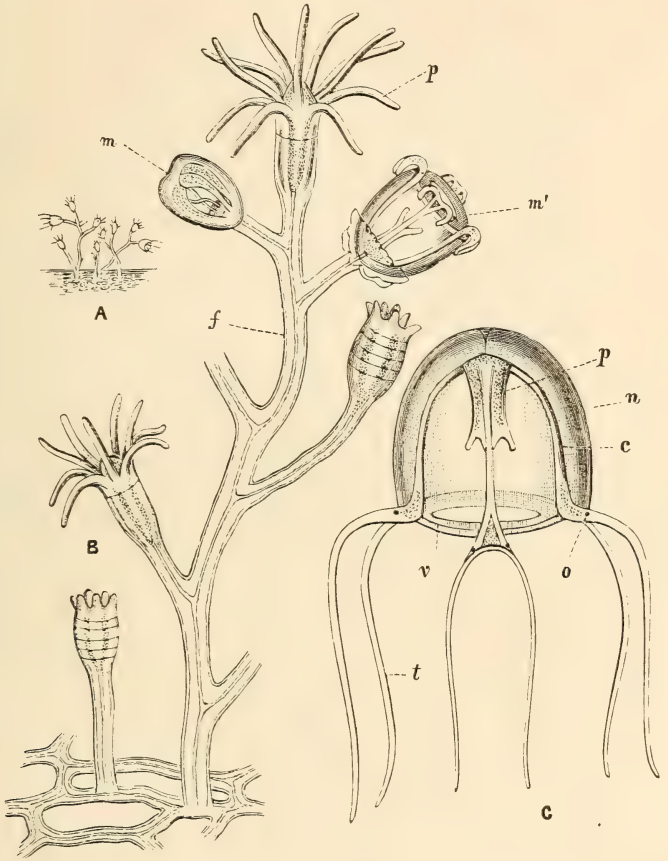

Fig. 77.—A, Part of the colony of *Bougainvillea muscus*, one of the composite Hydrozoa, of the natural size. B, Part of the same enlarged; *p*, A polypite fully expanded; *m*, An incompletely developed medusiform bud; *m'*, A more completely developed medusiform bud; *f*, Cœnosarc with its investing periderm and central canal. C, A free medusiform gonophore of the same; *n*, Gonocalyx; *p*, Manubrium; *c*, One of the radiating gastro-vascular canals; *o*, Ocellus; *v*, Velum; *t*, Tentacle. (After Allman.)

rhiza," by which it can attach itself to foreign bodies. At the opposite or "distal" end of the body is the opening of the mouth (fig. 76, *m*), surrounded by a variable number of hollow, extensile and tactile processes or "tentacles." The body-wall is composed of

an outer and inner membrane, known respectively as the "ectoderm" and "endoderm," and no hard external layer is produced. The mouth opens into a cylindrical body-cavity or "cœlenteric space," which runs the whole length of the body, and is completely undivided, no gullet being developed. There are, therefore, no radiating membranous partitions corresponding with the "mesenteries" of the *Actinozoa*. The animal can produce buds, which become developed into new "polypites," but these do not remain attached to the parent polypite, and the organism does not, therefore, become composite. Moreover, at certain seasons, the animal develops true reproductive organs, which have the form of external buds. These discharge the reproductive elements by rupture of their walls, but are not themselves separated from the organism.

The ovum in all the *Hydrozoa* gives rise to a "polypite" similar in structure to the entire organism in *Hydra;* but the primordial polypite is often endowed with the power of throwing out buds which remain, some or all of them, permanently united with the original "zoöid." In this way is produced a composite organism (fig. 76, B, and fig. 77), consisting of a greater or smaller number of zoöids or "polypites," united by a common fleshy stem or "cœnosarc." Very generally, the zoöids become differentiated into two sets, which differ in structure and in the part they play in the life of the colony. In the one series the zoöids constitute the ordinary nutritive "polypites" of the colony (fig. 77, *p*), and are concerned with supplying food to the organism. In the other series the zoöids—now spoken of by the general name of the "gonophores"—have a reproductive function, and are concerned with the production of the generative elements. These generative zoöids or "gonophores" may remain permanently attached to the parent colony (fig. 76, B), or they may become much modified and may become detached to lead a free existence (fig. 77). In this latter case, the detached generative zoöids usually present themselves in the form of "Jelly-fishes" or "Medusoids."

The colonies of the composite *Hydrozoa* are sometimes free, the proximal end of the cœnosarc not being adapted for fixation (as in the *Siphonophora* and the *Graptolitoidea* proper). In other cases the colony is attached to some foreign body by a modified proximal extremity or "hydrorhiza" (fig. 76, *rh*).

In a number of the composite *Hydrozoa* no hard structures in the shape of an external skeleton are developed. In many cases, however, the ectoderm secretes a firm horny outer layer or "periderm" (fig. 76, *pe*), which may cover the cœnosarc only (as in *Bougainvillea*, fig. 77), or may be extended into little cups or "hydrothecæ" within which the individual polypites are contained. When "hydrothecæ" are present, the body of the polypite is contained within the cup, and the distal extremity, with the mouth and tentacles,

can be protruded from the terminal opening or "aperture" of the hydrotheca (fig. 76 B, *h*). In some cases, not only are the nutritive polypites protected within "hydrothecæ," but the generative buds or gonophores are also provided with a horny or chitinous covering, constituting what are known as "gonangia." Lastly, in the group of the Hydrocorallines, and in a few other cases, the colony has the power of secreting carbonate of lime, and thus of giving rise to a calcareous skeleton, which in many cases is superficially similar to the "corallum" of certain of the *Actinozoa*.

With regard to the distribution of the *Hydrozoa* in *space*, the great majority of the organisms included under this head are marine, but in a few cases (*e.g.*, *Hydra*) the organism is found in fresh water. As to the general distribution of the class in *time*, the Fresh-water Polypes (*Hydrida*), the Oceanic Hydrozoa (*Calycophoridæ* and *Physophoridæ*), and the *Calycozoa* (*Lucernaria*, &c.) have left no traces of their past existence, as might have been anticipated from their want of hard parts. The *Trachymedusæ* and *Acraspeda* (Jelly-fishes and Sea-blubbers) are equally destitute of hard structures, and their absence from the palæontological record might have been confidently predicted. Under favourable circumstances, however, these soft-bodied organisms are capable of leaving impressions in soft mud or sand, by which their past existence may be determined; and such impressions have been recognised in deposits even as ancient as the Cambrian. The great group of the *Graptolitoidea* is not only entirely extinct, but is wholly restricted to the older Palæozoic rocks. The equally great group of the *Stromatoporoidea* is also extinct, and is principally confined to the earlier Palæozoic deposits, though fossils which are probably referable here are also found in the Mesozoic rocks. The *Corynida* and *Thecaphora*, both largely represented in recent seas, have left but few and imperfectly connected traces of their existence in past time; and some of the forms usually referred to these orders, and especially the more ancient ones, are of more or less dubious affinities. The recent genus *Hydractinia*, among the *Corynida*, occurs, however, in rocks as old as the Cretaceous. Lastly, the existing group of the Hydrocorallines is represented by fossil forms, which begin as early as the Trias.

In the following more detailed summary of the main divisions of the *Hydrozoa* and of their principal fossil forms, those groups which, as above mentioned, are not known to be represented in past time are left out of account.

Sub-class Hydroida.

The sub-class of the "Hydroid Zoophytes" comprises a large number of *Hydrozoa* in which the organism is attached, or is cap-

able of attachment, to foreign bodies by means of a modified proximal extremity or "hydrorhiza." A few of the types included in this sub-class are simple (*e.g.*, *Hydra*), but the organism consists

Fig. 78.—Recent Corynida. A, Portion of the colony of *Perigonimus minutus*, with polypites and reproductive buds, enlarged about 25 diameters; B, A single polypite of *Bimeria vestita*, greatly enlarged, showing the extension of the polypary upon the bases of the tentacles. (After Allman.)

typically of numerous simple polypites united by a branched "cœnosarc," and forming a plant-like or encrusting colony. Very

usually, the colony develops hard structures ("polypary" or "cœnosteum"), which may have the form of an external chitinous layer, or, in some instances, is composed of carbonate of lime. Reproduction takes place by fixed generative buds, or by the development of free reproductive zoöids ("gonophores").

Of the orders of the Hydroid Zoophytes, the only three which have fossil representatives are the *Corynida*, the *Thecaphora*, and the *Trachymedusæ*.

Order 1. Corynida.—The "Tubularian Zoophytes" or *Corynida* are mostly composite, forming more or less plant-like, or encrusting colonies, fixed to foreign objects proximally, and usually furnished with a skeleton or "polypary." The skeleton is mostly in the form of a chitinous investment, which encloses the cœnosarc (fig. 78, A), but which is not developed into definite cups or "hydrothecæ" for the reception of the individual polypites. In some cases, however, the skeleton consists of zoöidal tubes, in which the polypites were lodged, united by a general clathrate or tubulated cœnosarcal skeleton, as in the genus *Hydractinia* and its fossil allies. In the living genus *Bimeria*, also, the polypary forms an investment for the polypites, and is even prolonged upwards as far as the bases of the tentacles fig. 78, B). Though the skeleton of the *Corynida* is usually chitinous in composition, it is occasionally calcareous (as in some species of *Hydractinia* and in the genus *Parkeria*).

There are many recent types of the *Corynida*, such as the common Pipe-corallines (*Tubularia*), which, from the nature of their skeleton, might quite well have been preserved in the fossil condition. The only recent genus, however, of which any fossil representatives are known is *Hydractinia*, the colonies of which are well known as forming crust-like investments upon shells. The species of *Hydractinia* form chitinous—or rarely calcareous—crusts upon the exterior of the shells of Gastropods (fig. 79, A), the shell thus affected being often ultimately more or less largely dissolved away, and replaced by the substance of the parasite. The skeleton of *Hydractinia*, when fully grown, consists of numerous close-set vertical columns ("radial pillars," fig. 79, D *p*), which are united at irregular intervals by horizontal "laminæ," the number of these, and the consequent thickness of the crust, varying in different individuals or in different species. The successive "laminæ" are separated by narrow intervals or "interlaminar spaces" (fig. 79, *i*), which are broken into irregular chambers by the ascending "radial pillars." The "laminæ" themselves are not continuous membranes, but are formed by the anastomosis of numerous horizontal connecting-processes or "arms" (fig. 79, E *c*), which spring from the radial pillars at tolerably regular intervals. The "laminæ" are thus more or less cribriform, the apertures in their substance serving as tubes for the

zoöids of the colony, while the interlaminar spaces are filled with the soft cœnosarc. The surface of the skeleton is covered with projecting wart-like tubercles, interspersed with larger pointed spines (fig. 79, B and C), these being really the upper projecting ends of the "radial pillars." The surface also shows (fig. 79, B) the rounded pores which lodged the zoöids, together with singular branched grooves or open canals, which apparently serve for the lodgment of processes of the cœnosarc. In the living species of

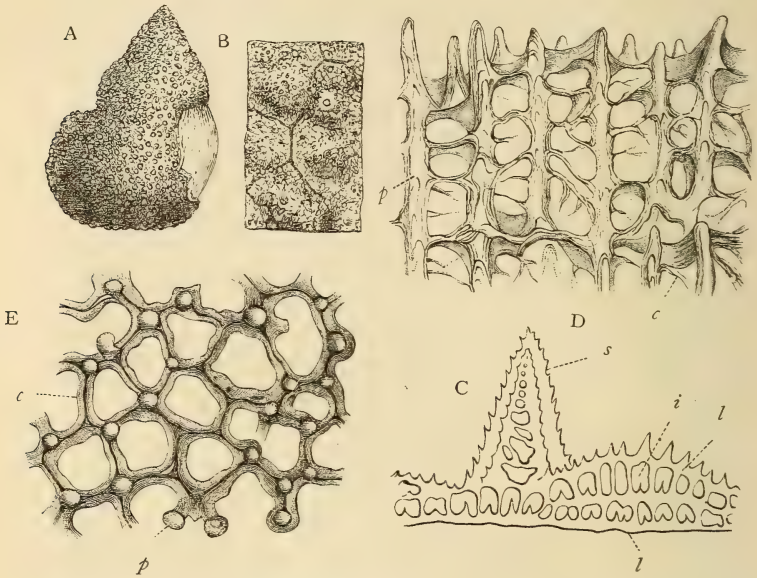

Fig. 79.—A, A colony of *Hydractinia pliocæna*, attached to the shell of a Gastropod, of the natural size, Pliocene. B, Portion of the surface of the same enlarged, showing wart-like prominences, branched cœnosarcal canals, and minute circular zoöidal apertures. C, Vertical section of the crust of the recent *Hydractinia echinata*, showing surface-tubercles and spines (*s*). The successive laminæ of the skeleton (*l*, *l*) are separated by "interlaminar spaces" (*i*) which are broken up into irregular chambers by "radial pillars." D, Vertical section of the crust of *Hydractinia echinata*, greatly enlarged, showing its composition out of vertical processes ("radial pillars") united by horizontal bars or "arms" (*c*). E, Horizontal section of the same, showing the pillars (*p*) and their connecting-processes (*c*), greatly enlarged. (After Allman, Carter, and the Author.)

Hydractinia the organism consists of the general crust-like cœnosarc, and of a large number of "polypites" emitted from the surface of the same. Many of these polypites have mouths and tentacles, and are devoted to the nutrition of the colony; others are non-tentaculate, and carry sac-like generative buds, which are not detached from the parent-colony; while others form long spirally coiled filaments, apparently intended for defensive purposes.

The recent species of *Hydractinia* are all marine, and the skeleton is in general composed of chitine; but in an African species, de-

scribed by Mr Carter, the skeleton is calcareous. The earliest known fossil forms of *Hydractinia* appear in the Cretaceous rocks, and a number of Tertiary forms are known. In the *Hydractinia circumvestiens* of the Pliocene Tertiary (which is probably identical with the *H. pliocœna* of Dr Allman), the skeleton is calcareous, and forms thick crusts upon the shells of Gastropods (fig. 79, A). The genera *Thalaminia* (Jurassic and Cretaceous) and *Sphæractinia* (Jurassic) have been founded by Steinmann for forms apparently allied to *Hydractinia*, and it is not impossible that the Jurassic genus *Ellipsactinia*, of the same author, should likewise be placed here.

In many respects related to *Hydractinia* is the singular Mesozoic genus *Parkeria*, best known by the *Parkeria sphærica* of the Greensand of Cambridge. The organism in *Parkeria sphærica* (fig. 80) is globular in form, and varies in diameter from a quarter of an inch or less up to more than two inches, the surface being often nodulated or covered with small rounded or elongated elevations. The skeleton must have been free in its adult condition, as a rule at any rate; but in many cases it grew round some foreign body, such as a fragment of shell. As to its chemical composition, there is no sufficient reason to doubt that the skeleton was originally composed of carbonate of lime, though many specimens are now found to be more or less largely phosphatised. As regards its minute structure, the skeleton is found, when examined microscopically by means of thin sections, to be composed of a characteristic minutely tubulated tissue, the tubules of which are radial in arrangement. This tubulated tissue is built up into a set of radiating columns ("radial pillars," fig. 81, *p*) and a series of concentrically disposed lamellæ, the latter being separated by interspaces ("interlaminar spaces"), which are broken up into irregular "chamberlets" (fig. 81, *c*). The tubulated tissue of the "radial pillars" is traversed by a variable number of comparatively wide, circular or oval tubes, which open upon the surface, or into the chamberlets—each successive row of chamberlets having at one time formed the surface of the skeleton—and which may be regarded as having lodged the nutritive polypites of the colony. Upon the whole, *Parkeria* may be regarded as representing an aberrant type of the *Hydractiniidæ*, but the genus has also relations to the Hydrocorallines. The little spheroidal fossils

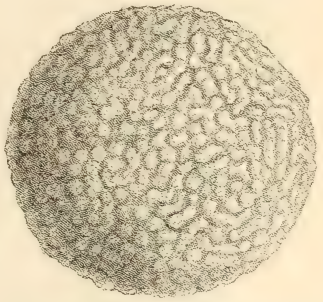

Fig. 80.—A large specimen of *Parkeria sphærica*, from the Upper Greensand of Cambridge, of the natural size. (Original.)

from the Chalk which have been placed in the genus *Porosphæra* have often been regarded as related to *Parkeria*, but their minute structure would rather support their being placed among the Sponges.

In connection with the preceding, a few words may be said with regard to the singular genera *Mitcheldeania* and *Solenopora*, which are of doubtful affinities, though the balance of evidence is in favour of referring them to the *Hydrozoa*. The genus *Mitcheldeania* comprises small

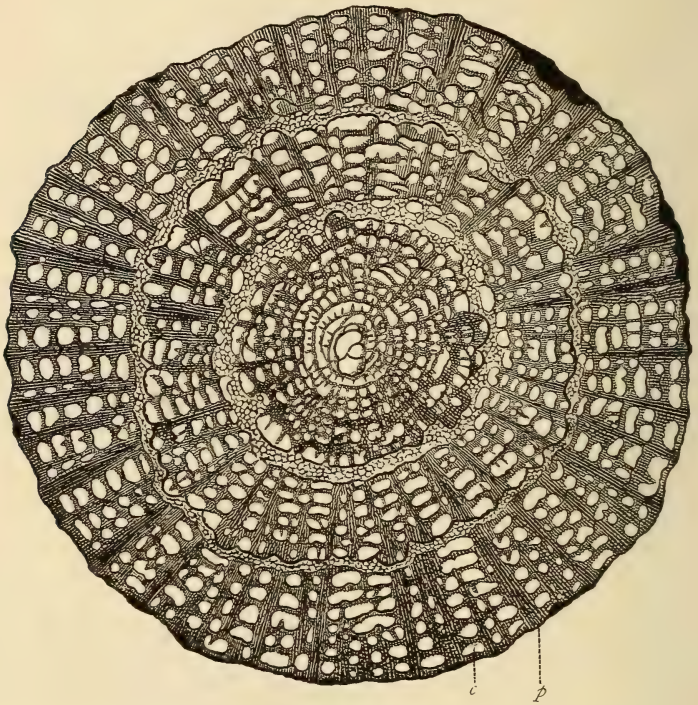

Fig. 81.—Vertical section across the centre of a specimen of *Parkeria*, enlarged twice. *p*, One of the radial pillars; *c*, One of the chamberlets. (Original.)

spheroidal fossils rarely reaching half an inch in diameter, which sometimes occur in such vast quantities as to give rise to actual beds of the Carboniferous Limestone (fig. 82). When examined microscopically, the skeleton of *Mitcheldeania* is found to be formed of radiating capillary tubes, which are disposed in concentric strata, and have a diameter of from $\frac{1}{12}$ to $\frac{1}{15}$ of a millimetre. These tubes have porous walls, and are united by a still more minutely tubulated tissue; but the structure of the organism is too complex to be advantageously discussed here.

The genus *Solenopora* comprises calcareous organisms of varying size, usually ranging from the dimensions of a pea up to those of an

orange, and of irregular shape (fig. 83, A). Examined microscopically, the organism in *Solenopora* is found to be wholly composed of radiating

Fig. 82.—A fragment of limestone rom the Lower Carboniferous Series of the south of Scotland, largely composed of *Mitcheldeania gregaria*, of the natural size. (Original.)

capillary tubes, arranged in concentric strata. The tubes (fig. 83, D) vary from $\frac{1}{12}$ to $\frac{1}{20}$ millimetre in size, and are in direct contact throughout, no interstitial tissue of any kind being developed. The tubes are irregular

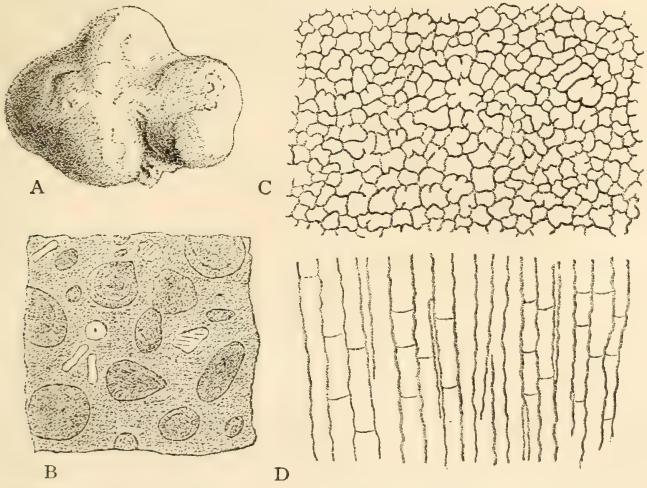

Fig. 83.—A, A small specimen of *Solenopora compacta*, Billings, from the Ordovician rocks of Saak, Esthonia, of the natural size; B, Surface of a piece of limestone largely made up of small specimens of the same, from the same locality, of the natural size; C, Tangential section of the same, enlarged about 35 times; D, Vertical section of the same, similarly enlarged. (Original.)

in form, with thin, often undulated walls, which are not pierced by any apertures or pores, but are often crossed by more or fewer transverse

partitions or "tabulæ" (fig. 83, D). Very commonly the tubes exhibit more or fewer inwardly directed partitions, which extend to a greater or less distance into the cavity of the tube, and are the result of the cleavage or "fission" of the tubes. The species of *Solenopora* are entirely confined to the Ordovician rocks, and sometimes occur in such profusion as to give rise to beds of limestone. The best known species (viz., *S. compacta*) has been recognised in the Ordovician limestones of Russia, Britain, the United States, and Canada.

Both *Mitcheldeania* and *Solenopora* are remarkable for the extraordinary minuteness of their component tubes, and in this respect they differ from all known Cœlenterates. Apart from this feature, they present in their structure a general resemblance to forms like *Parkeria*, and they

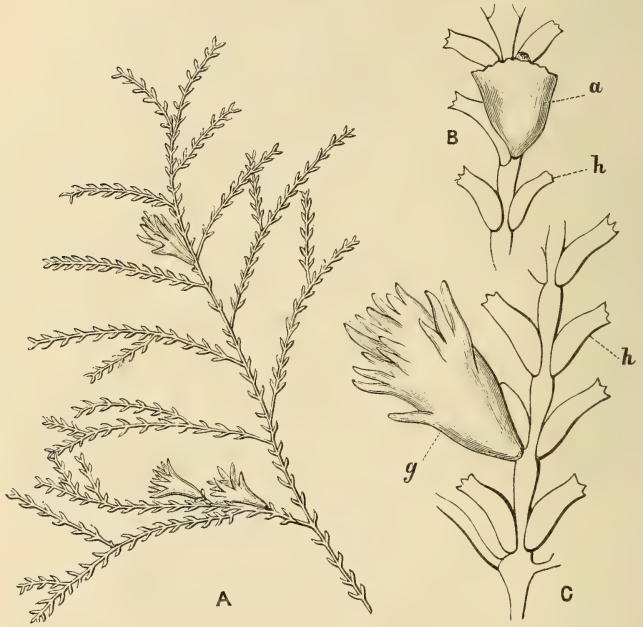

Fig. 84.—Sertularida. A, Portion of the colony of *Diphasia* (*Sertularia*) *tamarisca*, of the natural size, showing hydrothecæ and female ovarian capsules (gonangia). B and C, Portions of different branches of the same, enlarged: *h*, Hydrothecæ; *a*, Male gonangium; *g*, Female gonangium. (After Hincks.)

may therefore be provisionally placed among the Hydroid Zoophytes. In some points, however, the genus *Mitcheldeania* would appear to be rather related to the Hydrocorallines.

Among the other forms which have been referred to the *Corynida* are the genera *Corynoides* and *Palæocoryne*. The former of these may, perhaps, be best regarded as an abnormal type of the *Graptolitoidea*, and will be alluded to in speaking of these organisms. The genus *Palæocoryne*, on the other hand, is founded upon structures which belong to the fronds of certain of the *Fenestellidæ*, and it will therefore be treated of in dealing with the *Polyzoa*.

Order 2. Thecaphora.—This order includes the Sea-firs and their allies (*Sertularida* and *Campanularida*), in which the organism is fixed, and consists of a more or less plant-like colony (fig. 84, A), composed of numerous polypites united by a common stem or "cœnosarc." The cœnosarc usually consists of a main stem or "hydrocaulus," with many branches, and it is fixed to foreign bodies by an adherent base or "hydrorhiza." The colony produces a strong corneous or chitinous outer investment (the "periderm" or "polypary"), which not only invests the cœnosarc, but is also prolonged into cup-like receptacles, which enclose the individual polypites, and are known as the "hydrothecæ." The reproductive zoöids ("gonophores") are either set free as Jelly-fishes (as in the Campanularians generally), or are developed within urn-like receptacles ("gonangia" or "gonothecæ"), which are of larger size than

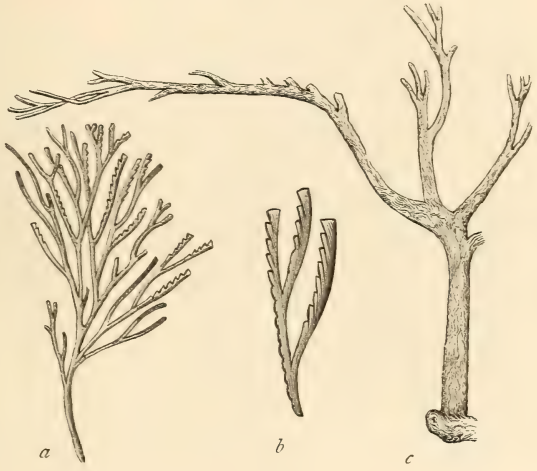

Fig. 85.—*Dendrograptus Hallianus*. *a*, Portion of the frond, natural size; *b*, Portion of a branch, enlarged; *c*, The footstalk and some of the principal branches, natural size. Upper Cambrian (Potsdam Sandstone). (After Hall.)

the ordinary hydrothecæ (fig. 84, B and C). In this latter case, the reproductive zoöids are not liberated from the parent colony as independent organisms. In the typical Sertularians, the hydrothecæ spring directly from the sides of the cœnosarc and are not supported on stems, and they may be biserial (as in *Sertularia* and *Diphasia*, fig. 84, A), or they may, as in *Plumularia* and its allies, be developed on one side only of the divisions of the cœnosarc. On the other hand, in the Campanularians the polypites are stalked and terminal, each being placed at the end of a division of the cœnosarc.

The existing *Thecaphora* are not only very abundant and very

widely represented in recent seas, but they possess a chitinous polypary which seems to be quite as well suited for preservation in fine-grained sediments as is that of the Graptolites. It is therefore a matter difficult of explanation that, except in late Quaternary deposits, no trace of an absolutely undoubted Sertularian or Campanularian, similar to the ordinary existing forms of the order, has been as yet discovered. On the other hand, the ancient Palæozic deposits have yielded the remains of various extinct organisms, which have often been referred to the *Graptolitoidea*, but which, with greater probability, may be regarded as early types of the *Thecaphora*. One of the most interesting of these is the Cambrian and Ordovician genus *Dendrograptus*, in which the organism had the form of a spreading

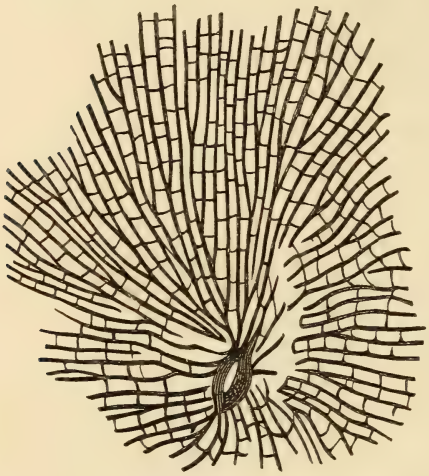

Fig. 86.—*Dictyonema retiforme*, Hall. Silurian (Niagara Group), United States. (After Hall.)

Fig. 87.—A branch of *Ptilograptus plumosus*, Hall. Enlarged. Ordovician (Quebec Group), Canada. (After Hall.)

and branched frond, furnished with a strong footstalk (fig. 85), by which it was probably attached to some foreign body. The branchlets carry upon one side a series of little chitinous cups or "hydrothecæ" ("cellules"), which agree with the similar structures of the Graptolites in partially overlapping one another.

In *Dictyonema* (fig. 86) we have organisms resembling *Dendrograptus* in many respects, but not possessing any footstalk. The frond is branched and plant-like, and is fan-shaped or funnel-shaped in form. It is not certainly known whether the organism was attached by its base or not; but there is the strongest probability in favour of its having been fixed. The branches radiate from the base, running nearly parallel with one another, and often bifurcating. They are united to one another at short intervals by numerous, irregular,

slender, transverse processes or dissepiments, and they bear small horny cups or "hydrothecæ" ("cellules") like those of the Graptolites. *Dictyonema* ranges from the Upper Cambrian to the Middle Devonian. The genus bears a close superficial resemblance to the *Fenestellæ* or Lace-corals (belonging to the *Polyzoa*); but the latter have a calcareous skeleton, and have no "hydrothecæ." Besides the above-mentioned genera, *Callograptus* and *Ptilograptus* (fig. 87) may with great probability be referred to the *Thecaphora;* as may, perhaps, be the obscure fossils *Buthograptus* and *Thamnograptus*. All these genera are found in the Ordovician or Silurian rocks.

Oldhamia.—The singular structures described under the genus *Oldhamia* may be noticed here, as they have been referred to the *Hydrozoa;* though their true nature is altogether uncertain. *Oldhamia* occurs in certain green and purple grits of Lower Cambrian age, at Bray Head, in Wicklow, Ireland, where the supposed fronds are found in great abundance, matted together, and spreading over the surfaces of the strata. A form of *Oldhamia* is also said to occur plentifully in the Potsdam Sandstone (Upper Cambrian) of Wisconsin, in North America, and still another form has been described by Barrois from the Cambrian rocks of the Pyrenees. *Oldhamia antiqua*, the commonest form, consists of a central thread-like axis from which spring bundles or umbels of short radiating branches (fig. 88), at regular intervals; whereas in the so-called *Oldhamia radiata* the branches radiate from a central point in all directions. *Oldhamia* has been variously referred to the Sertularian Zoophytes, to the *Polyzoa*, and to the *Algæ*. It has not, however, been as yet satisfactorily shown that *Oldhamia* is truly organic, and it is quite possible that the structure so called is the result of purely inorganic agencies. If really organic, it would seem more than probable that *Oldhamia* is referable to the vegetable kingdom, and that it belongs to the *Algæ*. This is the view held by Barrois, who compares *Oldhamia* with some of the types of *Algæ* which are placed in the family of the *Dasycladeæ*.

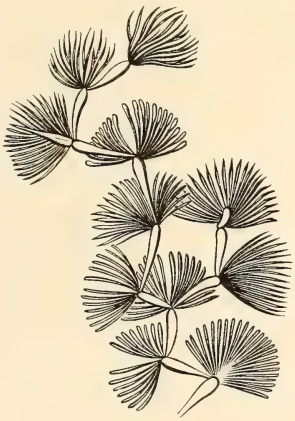

Fig. 88.—*Oldhamia antiqua*, natural size (after Salter). Cambrian.

Order 3. Trachymedusæ. — The *Trachymedusæ* constitute a peculiar group of the "Jelly-fishes," which agree with all the organisms grouped under this popular designation in the possession of a gelatinous swimming-bell, from the under side of which is suspended a single "polypite." From the margin of the swimming-bell depend

solid tentacular processes, and the substance of the bell is traversed by simple radiating canals which communicate above with the gastric cavity of the polypite. The reproductive organs are developed in the course of the radiating canals of the disc, and the embryo is developed directly into the adult form, without the intervention of an intermediate fixed and sexless stage.

Though wholly devoid of hard structures, the *Trachymedusæ*, as will be more fully pointed out in dealing with the *Acraspeda*, are capable of leaving traces of their past existence in the form of impressions left by their stranded bodies in fine mud. Impressions of this nature have been recognised in the fine-grained lithographic limestone (Jurassic) of Solenhofen, in Bavaria, and have been referred to the genera *Palægina* and *Trachynemites*, representing respectively the two existing groups of the *Æginidæ* and *Trachynemidæ*.

Sub-class Lucernarida.

The division of the *Lucernarida* comprises a large number of recent *Hydrozoa* in which the base of the organism is developed into a disc-shaped or cup-like structure (the "umbrella"), in the walls of which the reproductive organs are developed, and which carries on its concave side a single, more or less modified "polypite." The "Jelly-fish" thus constituted may develop itself directly, or it may be only the generative form of a minute fixed organism ("Hydra-tuba"), from which it is produced by fission.

The peculiar group of Lucernarians (*Calycozoa*) of which *Lucernaria* itself is the type, is wholly unrepresented by fossil forms, and needs no further consideration here. On the other hand, the group of the *Acraspeda*—or, as it is often called, *Discophora*—has left various traces of its past existence, and is in many ways of palæontological interest. The group of the *Acraspeda* comprises most of the larger organisms which are usually spoken of as "Jelly-fishes," though the structures so called are for the most part merely the generative zoöids produced by a minute sexless Lucernarian. Such a Jelly-fish (as, for example, the recent *Aurelia*) consists of a great gelatinous swimming-bell or "umbrella," from the under side of which hangs a single polypite, the structure of which is greatly modified in the *Rhizostomidæ*. The swimming-bell is traversed by a complex system of canals, connected superiorly with the gastric cavity of the polypite (fig. 89), and its margin usually carries more or fewer "tentacles," which are often of great length. The mouth of the polypite is extended into fringed or lobed processes, often of great length (fig. 89, *l*). Lastly, the reproductive organs are in the form of four folded bands, which project into four special cavities (the "sub-genital pouches") in the floor of the gastric cavity.

The Acraspedote Jelly-fishes are wholly marine, and are often of very large size. They usually swim near the surface, but they have been observed to crawl about on the sea-bottom in shallow water, and they have also been seen to lie at the bottom with the base of the umbrella turned downwards and the tentacles directed upwards. Though they possess no hard structures, and though their tissues are saturated with water, and therefore singularly perishable, they are nevertheless capable of producing impressions in sand or mud by which their past existence, and even their form, may be determined.

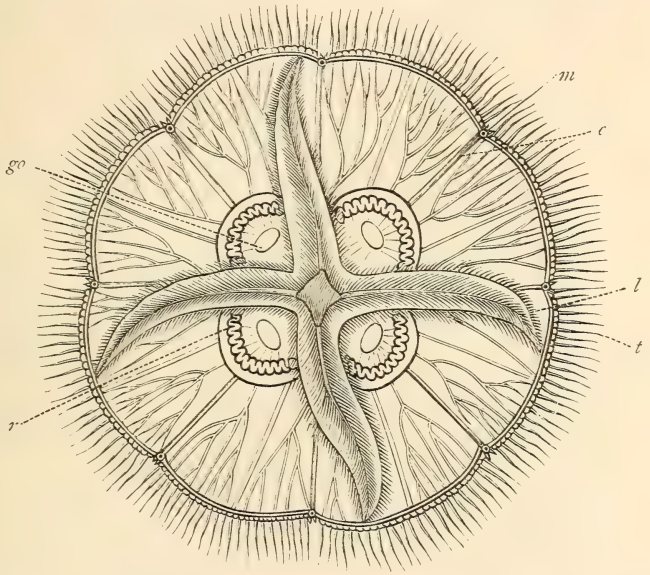

Fig. 89.—Under side of the umbrella of *Aurelia aurita*, one of the Acraspedote Medusæ, reduced in size. *l*, One of the four oral lobes, in the centre of which is placed the mouth; *t*, Tentacles attached to the margin of the umbrella; *c*, One of the radiating canals of the umbrella; *m*, Sense-organ; *r*, Reproductive organ, projecting into a "sub-genital pouch" (*go*). (After Claus and Sedgwick.)

The markings by which the former existence of Jelly-fishes may be recognised are of different kinds in different cases. In one group of cases the body of the Jelly-fish has fallen after death upon the fine mud of the sea-bottom, or has been thrown up on the shore, and an impression representing the swimming-bell, and in some cases the tentacles, of the animal, has thus been formed in the soft sediment. Upon impressions of this nature in the lithographic slates (Jurassic) of Solenhofen, Haeckel has founded various genera. Some of these, as previously noted, are believed to belong to the group of the *Trachymedusæ;* but others, such as *Rhizostomites* (fig. 90) and

Hexarhizites, are considered as referable to the *Acraspeda*, and to be related to such living types as *Rhizostoma*.

Of a somewhat more questionable nature are the singular bodies from the Cambrian rocks of Sweden, to which Nathorst has given the name of *Medusites*. These bodies are usually in the form of four-rayed or five-rayed stars, or have the shape of four-sided or five-sided pyramids the angles of which are more or less prolonged; and they have no actual organic structure. By Nathorst, however, they are regarded, with much probability, as being produced by the infilling of the cavities of dead Jelly-fishes with mud or sand. On this view the central pyramidal body of *Medusites* represents the cast

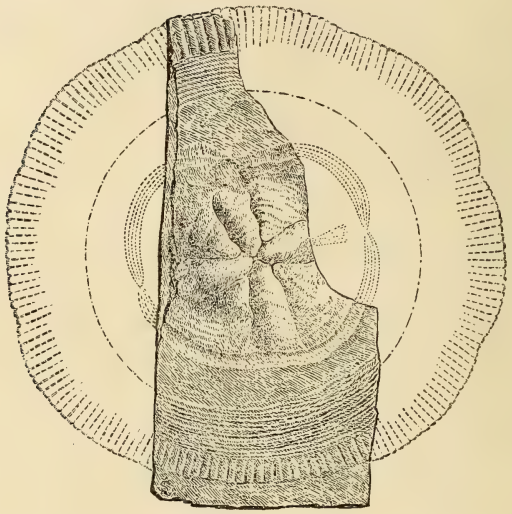

Fig. 90.—The impression of the swimming-bell or a Jelly-fish (*Rhizostomites admirandus*) preserved in the lithographic slate (Jurassic) of Eichstadt, in Bavaria, one-seventh of the natural size. The missing parts are restored in outline. (Copied from Zittel.)

of the gastric cavity of the polypite, while the four or five arms which radiate from this represent casts of the radiating angles of the mouth. In support of this view, Nathorst points to the known habit of certain Jelly-fishes of lying at the bottom with the umbrella turned down and the mouth directed upwards, in the position figured in fig. 89, and he shows how this would naturally facilitate the filling of the gastric cavity with mud. Moreover, Nathorst has shown that bodies exceedingly similar in form and marking to the Cambrian *Medusites* can be produced by taking casts of the internal cavities of fresh specimens of Jelly-fishes in dilute plaster of Paris.

Lastly, Nathorst has brought forward evidence to show that Jelly-fishes are capable of producing various peculiar markings by their

movements when creeping about on the muddy bottom of the sea in shallow water, or by the trailing of their tentacles over soft sediment. In view of this evidence, he has suggested that the peculiar striated and furrowed markings in the Cambrian rocks ("Fucoidal Sandstone") of Sweden which have been described under the name of *Eophyton* (fig. 91), are to be regarded as really produced by the trails of Jelly-fishes. These peculiar markings were originally described as the remains of land-plants, but it seems certain that this

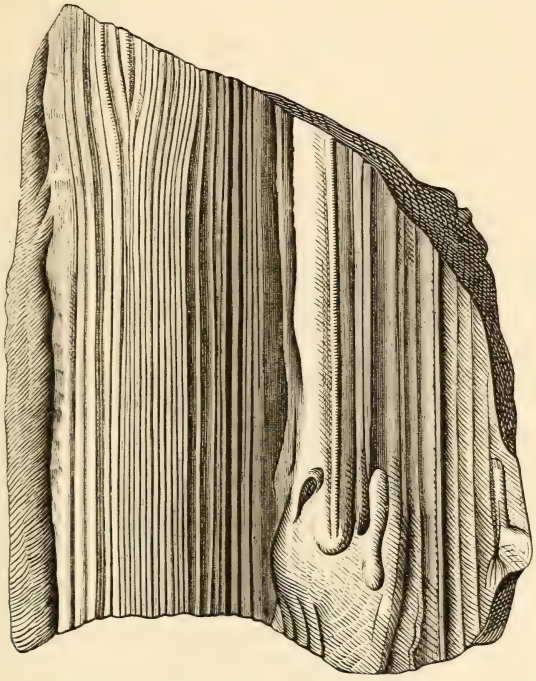

Fig. 91.—Fragment of *Eophyton Linneanum*. Lower Cambrian.

cannot be their real nature. Nathorst has, in fact, produced precisely similar markings by allowing plants to trail over soft mud; and if the so-called *Medusites* of the Swedish Cambrian is rightly regarded as founded on the casts of the gastric cavity of Jelly-fishes, we have in these a proof that there existed at the time animals capable of producing the striated trails of the same deposits to which the name of *Eophyton*[1] was originally applied.

[1] The fossil described by Hicks from the Cambrian rocks of Wales under the name of *Eophyton explanatum* has been shown by Hinde to be really the anchoring-rope of a Hexactinellid Sponge.

CHAPTER XIV.

HYDROZOA — Continued.

Sub-class Graptolitoidea.

The organisms comprised under the head of *Graptolitoidea* (the *Rhabdophora* of Allman) are commonly known as "Graptolites," and constitute a remarkable assemblage of extinct *Hydrozoa*, all the known forms of which are confined to the Upper Cambrian, Ordovician, and Silurian deposits. The Graptolites may be defined (if the abnormal genus *Corynoides* be excluded) as being composite *Hydrozoa* in which the organism consists of numerous polypites united by a cœnosarc; the latter being enclosed in a tubular, chitinous polypary, usually forming a complete external membrane of considerable strength, while the former were protected within "hydrothecæ." The polypary may be undivided or branched, and was invariably free, the organism apparently floating in the water with the proximal end of the colony directed upwards. In most cases, the polypary is strengthened by a peculiar rod-like axis (the "virgula"), which lies in a groove on the dorsal side of the polypary (*i.e.*, on the side opposite to that on which the hydrothecæ are developed), and may be prolonged beyond one or both ends of the colony. The polypary is, typically if not universally, furnished at its proximal end with a minute triangular or dagger-shaped body (the "sicula"), which represents the embryonic skeleton.

As regards its *development*, the earliest condition in which a typical Graptolite presents itself is that of a small triangular corneous body, which has been termed by Professor Lapworth the "sicula" (fig. 92, A), and which is the starting-point of the entire polypary. In its earliest stage (fig. 92, A *a*) the "sicula" is merely a triangular horny sheath lodging the cœnosarc, but a rod-like axis or "virgula" (fig. 92, A *b*) is soon developed along its entire length, often projecting freely at one or both extremities. In the next stage (fig. 92,

A *c*) a bud, constituting the first hydrotheca, appears on one side, near the thicker end of the "sicula." If the form under observation belongs to the group of Graptolites in which the polypary possesses two rows of hydrothecæ (the "diprionidian" Graptolites), a second bud next appears on the opposite side of the "sicula" to the first one, and a little in advance of it. In the further development of the polypary, the sicula appears to remain stationary, usually persisting

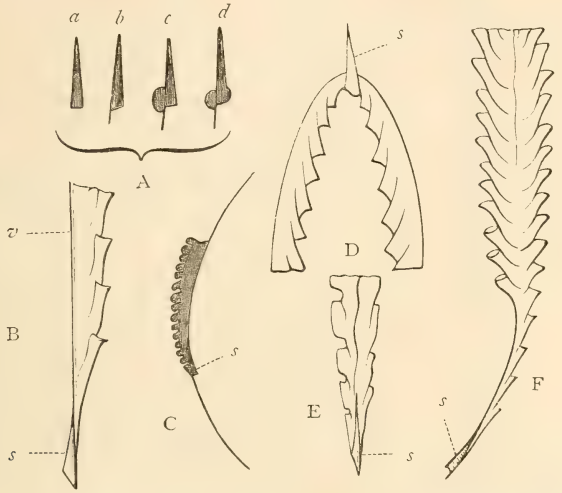

Fig. 92.—A, Early stages in the development of Graptolites: *a*, The earliest stage of the "sicula," in which no virgula is developed; *b*, Later stage, with a virgula; *c*, Still later stage, with a single primordial hydrotheca; *d*, Stage with two hydrothecæ. B, Base of *Monograptus gregarius*, enlarged; C, *Monograptus Clingani*, young specimen, of the natural size, showing a proximal and distal extension of the virgula; D, Proximal portion of *Didymograptus Murchisoni*; E, Proximal portion of *Climacograptus normalis*, enlarged; F, Proximal portion of *Dimorphograptus*, enlarged. *s* Sicula; *v* Virgula. All the specimens are Ordovician or Silurian. (Partly after Lapworth and Tullberg, and partly original.)

at the base of the organism as a dagger-shaped process, the broad end of which is directed proximally (fig. 92, B—F). In some cases the sicula becomes obsolete, or it may ultimately develop into a branch, or, rarely, into a vesicle (as in *Diplograptus physophora*).

Taking a simple Graptolite, such as *Monograptus priodon* (fig. 93), as the type of the sub-class, the polypary will be seen to consist of three principal morphological elements—viz., the cœnosarc, the hydrothecæ, and the virgula. The last mentioned of these—often spoken of as the "axis"—is one of the most characteristic of the structures of the Graptolitic polypary, and has the form of a cylindrical fibre or rod, probably hollow internally, which gives support to the flexible chitinous skeleton. It runs, in such types as *Monograptus*, along the dorsal side of the polypary, opposite to the hydro-

thecæ (fig. 93, B), whereas in the double Graptolites it occupies a central or sub-central position, between the two rows of hydrothecæ which form the biserial colony. In any case it lies in a groove in the periderm, and is really outside the cœnosarc. Very commonly, the virgula projects beyond one or both ends of the polypary as a longer or shorter naked rod (fig. 92, C, and fig. 94, A); the proximal extension being often spoken of as the "radicle," though this name has also been used for the "sicula." Running parallel with the virgula is the cœnosarc — often spoken of as the "common canal"—which is enclosed in the tubular periderm, and presents itself in compressed specimens as a flat space of variable width between the virgula and the bases of the hydrothecæ (fig. 94, *c*). Springing from the cœnosarc, lastly, is a series of chitinous cups or "hydrothecæ," which have often been spoken of as the "cellules" or "denticles." Each hydrotheca rests by its base upon the cœnosarcal canal, is separated from its neighbours by a definite partition, and opens at its apex by an "aperture," through which the contained polypite could protrude its tentaculate head. The hydrothecæ vary extremely in form and in the precise position of the aperture in different types of Graptolites, or in different species of the same genus (fig. 94); and the lip of the aperture may be variously ornamented with spines. Lastly, the hydrothecæ are typically so disposed that they more or less extensively overlap one another (fig. 94, B and C).

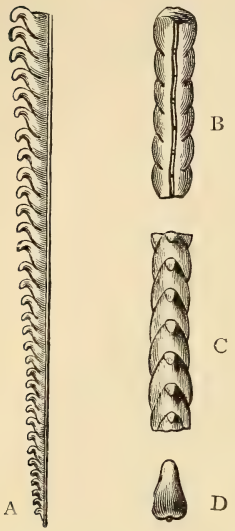

Fig. 93. — Morphology of *Monograptus priodon*. A, *Monograptus priodon*, Bronn, preserved in relief—lateral view slightly enlarged—from the Silurian rocks; B, Dorsal view of a fragment of the same species — considerably enlarged; C, Front view of a fragment of the same, showing the mouths of the hydrothecæ — much enlarged; D, Transverse section of the same. (Original.)

While the above is the arrangement of parts in such a form as *Monograptus priodon*, there are many departures from this typical condition in other forms of the Graptolites. Thus, the general periderm, instead of forming a dense continuous membrane, may, as in *Retiolites* (fig. 106), be reduced to a mere network of chitinous threads. In the same genus, the virgula is double, the two halves being placed on opposite sides of the cœnosarc, and being united with the peridermal network. Again, the hydrothecæ, instead of more or less largely overlapping one another, may, as in *Rastrites* (fig. 98), spring quite separately and at greater or smaller intervals from the cœnosarc. Lastly, it has not been certainly estab-

lished that the "virgula" is invariably developed in all types of the Graptolites, and the name of *Rhabdophora*, proposed for the group by Professor Allman, is, therefore, not wholly appropriate.

With regard to the *reproductive process* in the Graptolites there are strong grounds for supposing that the generative elements were developed in specially modified polypites, or "gonophores," after a manner analogous to that which occurs in the Hydroid Zoophytes generally. In some cases, these generative buds may have been destitute of a hard covering, and therefore incapable of preservation;

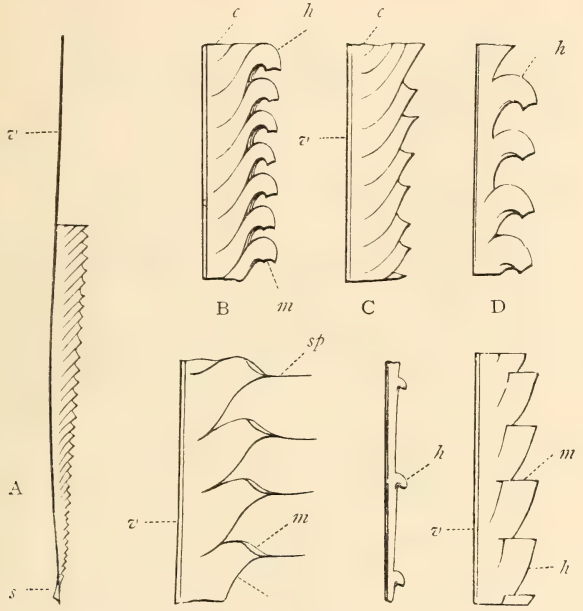

Fig. 94.—A, *Monograptus colonus*, enlarged; B, A fragment of *Monograptus priodon*; C, *Monograptus colonus*; D, *Monograptus Clingani*; E, *Monograptus spinigerus*; F, *Monograptus attenuatus*; G, *Monograptus Hisingeri*, all greatly enlarged. *s*, Sicula; *v*, Virgula; *c*, Cœnosarc; *h*, Hydrotheca; *m*, Aperture of hydrotheca; *sp*, Apertural spine. (After Lapworth.)

but in other cases there is evidence of the existence of chitinous receptacles, of larger size than the hydrothecæ, and of different form, which may be compared with the "gonangia" or "ovarian capsules" of the recent Sertularians, and may be supposed to have lodged the reproductive zoöids. Thus, occasional specimens of certain of the diprionidian Graptolites have been found to carry on their sides singular horny sac-like structures, which can hardly be regarded as anything else than as of the nature of "gonangia." Moreover, it is

very usual, as pointed out by the writer, to find in association with Graptolites peculiar, bell-shaped or conical, chitinous capsules, which may be spoken of by the general name of *Dawsoniæ* (fig. 95). These capsules present different appearances in accordance with the direction in which they have been compressed, and they vary in shape and size. Each is furnished with a little spine or mucro at its summit, and also with a marginal chitinous thread or fibre. These singular bodies have not hitherto been certainly detected in direct connection with the polypary of any Graptolite. They may, however,

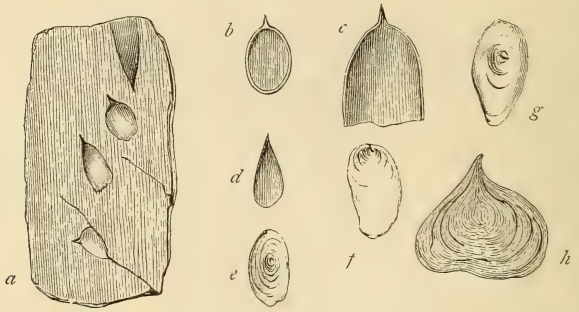

Fig. 95.—Various forms of bell-shaped chitinous capsules (*Dawsonia*) found associated with Graptolites, and supposed to be of the nature of "gonangia." (Original.)

be regarded, with great probability, as being of the nature of "gonangia," though they probably differed from the structures so called in the recent Sertularians in becoming detached from the parent colony.

Two leading *types of structure* may be distinguished amongst the Graptolites, and these may be respectively termed the "monoprionidian" and "diprionidian" type. The monoprionidian Graptolites (*Monoprionidæ*) are distinguished by the fact that, whether the colony be simple or branched, the hydrothecæ are arranged in a single series, and the cœnosarc is thus single and not double. In the typical *Monoprionidæ* the hydrothecæ are uniserial over the entire polypary (as in *Monograptus* or *Didymograptus*). A transition is, however, effected between the monoprionidian and diprionidian groups of Graptolites by such intermediate types as *Dimorphograptus* (fig. 92, F) in which the proximal portion is monoprionidian and the distal portion diprionidian, or *Dicranograptus* (fig. 103, A) in which the opposite state of things obtains. On the other hand, in the proper *Diprionidæ* the polypary is duplicate, and consists of two separate rows of hydrothecæ, which may spring from an undivided common cœnosarc, but which, more usually, arise from

two separate cœnosarcal tubes which are closely apposed to one another, back to back, along their entire length.

Before briefly considering some of the leading types of these two great groups, attention may be directed for a moment to the singular genus *Corynoides* (fig. 96), which differs in important respects from all the ordinary Graptolites. In this curious form the organism consists of a cylindrical chitinous tube, tapering towards the base, where it is furnished with two small spines, and expanding above into a species of toothed cup. The polypary does not show any signs of having been attached to any foreign body, and the suggestion has been thrown out by Lapworth, that the type may be regarded as a Graptolite which never proceeded beyond the stage of a "sicula."

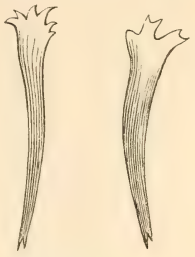

Fig. 96.—*Corynoides calicularis*, enlarged. (Original.)

The type of the Monoprionidian Graptolites is the genus *Monograptus* itself (figs. 93 and 94), which is also the central genus of the family of the *Monograptidæ*. In this genus the polypary is simple and linear, possessing but a single row of hydrothecæ on one side, and commencing by an attenuated, often curved base. The polypary is straight, curved, or helicoid in different forms; and great variations exist in the shape of the hydrothecæ in different species (fig. 94), these structures usually, but not always, overlapping to a greater or less extent. The "sicula" is attached along the dorsal margin of the proximal end of the polypary (fig. 92, B). All the species of *Monograptus* are confined to the Silurian rocks proper (the Upper Silurian of Murchison), ranging from the base to the summit of the system. In the allied genus *Cyrtograptus* (fig. 97) the polypary is also unilateral, in so far as the hydrothecæ are produced from the sicula in one direction only, but the polypary is now branched. This genus is also confined to the Silurian rocks proper. Again, in the genus *Rastrites* (fig. 98) the polypary resembles that of *Monograptus* in form, but the hydrothecæ are more or less linear,

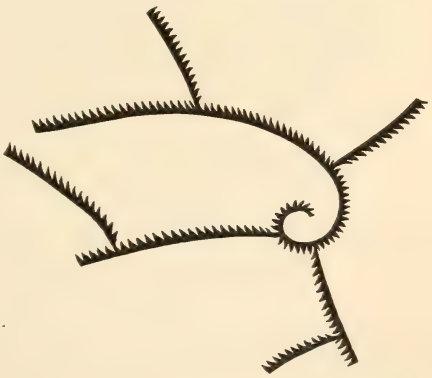

Fig. 97.—*Cyrtograptus Murchisoni*, Carr. (After Carruthers.)

and are isolated from one another, instead of overlapping. The species of this genus are, like those of the preceding genera, restricted to the Silurian rocks proper.

The family *Leptograptidæ* has been founded by Lapworth for a number of bilaterally-symmetrical branched Graptolites, which agree with one another in having the hydrothecæ attached along

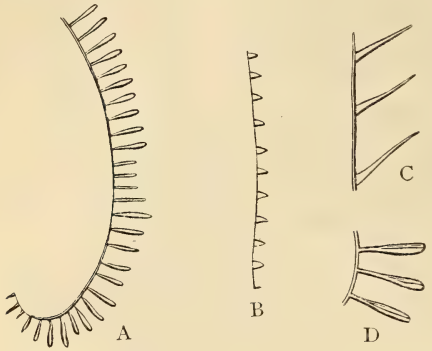

Fig. 98.—A, *Rastrites peregrinus*; B, *Rastrites capillaris*; C, *Rastrites Linnæi*; D, Fragment of *Rastrites peregrinus*, greatly enlarged. All the figures are magnified. Silurian. (Original.)

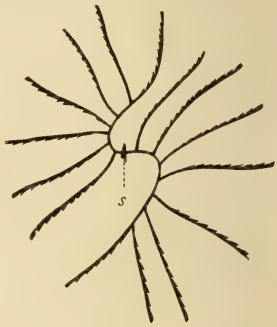

Fig. 99.—*Cœnograptus gracilis*, of the natural size. *s* Sicula. Ordovician. (After Lapworth.)

the whole of one face to the cœnosarc, and not overlapping. The form of the polypary varies much in this family, consisting of two long primary branches in *Leptograptus* itself, but being rendered complex in *Pleurograptus* by the development of secondary branches from each of the long primary stems, these in turn sometimes giving off tertiary branches. In the beautiful genus *Cœnograptus* (fig. 99), again, the two primary stems originate from the centre of a triangular sicula, and form an S-shaped frond, the convex sides of which give off simple branches. All the above genera are found in the Ordovician rocks, but do not extend upwards into the Silurian proper.

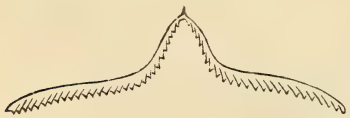

Fig. 100.—*Didymograptus V-fractus*. Ordovician (Skiddaw Slates).

The great family of the *Dichograptidæ* comprises a large number of branched Graptolites, all the forms of which are found in the Upper Cambrian and Ordovician deposits. The simplest type of this family is the genus *Didymograptus* (figs. 92, D, and 100), in which the polypary consists of two simple branches springing from a small pointed "sicula." The angle included between the polypiferous sides of the two branches ("angle of divergence") is always less than 180°, the opposite

angle ("sicular angle") being necessarily over 180°. The species of *Didymograptus* are confined to the Ordovician rocks. Closely allied to the preceding is the genus *Tetragraptus* (fig. 101) in which the polypary consists of four simple branches springing from a central, non-polypiferous connecting-process or "funicle," which bifurcates at each end. The base is sometimes provided with a peculiar corneous disc, similar to that which characterises various species of *Dichograptus*. The species of *Tetragraptus* are all Ordovician (Arenig). In the genus *Dichograptus* (fig. 102), again, the polypary consists of eight simple branches, which arise from the same number of divisions of a non-polypiferous basal process or "funicle." In many cases, the divisions of the "funicle" are enveloped in a species of horny "disc" or plate (fig. 102), which is believed to have been composed of two laminæ. The functions of this disc are doubtful, but it has been compared with the "float" of the Portuguese-Man-of-war (*Physalia*) or of *Velella* among the recent Oceanic *Hydrozoa*. The species of *Dichograptus* are confined to the lower portion of the Ordovician series (Arenig); but allied genera, in which the polypary is irregularly branched, are found in the Upper Cambrian deposits, and are represented in the Ordovician rocks.

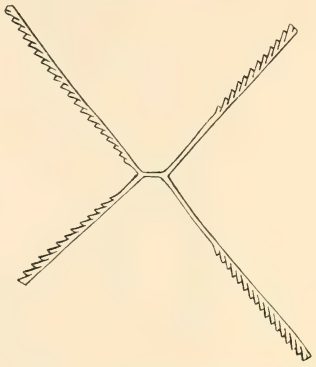

Fig. 101.—*Tetragraptus quadribrachiatus* (after Hall). Ordovician (Skiddaw and Quebec groups).

The only remaining family of the Monoprionidian Graptolites is that of the *Dicranograptidæ*, comprising the two genera *Dicranograptus* and *Dicellograptus*, in both of which the polypary is composed of two branches, and the terminations of the hydrothecæ are isolated and characteristically incurved, so as to bring the cell-apertures within the line of margin of the branch (fig. 103). In the genus *Dicellograptus* (fig. 103, B) the two branches of the polypary are wholly free, and diverge from a basal "sicula," in such a manner as to resemble the genus *Didymograptus*. The angle included between the polypiferous sides of the branches ("angle of divergence") is, however, greater than 180°, while the opposite angle ("sicular angle") is necessarily less than 180°. In the curious genus *Dicranograptus* (fig. 103, A) we have a transition between the Monoprionidian and Diprionidian groups of Graptolites, the two branches composing the polypary being adherent by their dorsal surfaces for a longer or shorter distance, and then diverging

freely. The species of both these genera are confined to the Ordovician rocks.

Coming next to the group of the Diprionidian Graptolites, the typical family is that of the *Diplograptidæ*, of which the type-genus is *Diplograptus* itself. In this genus the polypary (fig. 104) consists—as it does in most of the genera of the family—of two simple monoprionidian branches, which are closely united to one another along their flattened dorsal surfaces, but are enclosed in independent peridermal sheaths, and are therefore really separate. The virgulæ of the two branches coalesce, and form a single rod-like axis, which is embedded in a groove between the cœnosarcal sheaths, and commonly projects distally as a naked fibre, while it appears proximally as a shorter or longer "radicle" (figs. 104 and 105). In some of the *Diplograptidæ*, however, according to Lapworth, there is only a single cœnosarcal canal from which the two rows of hydrothecæ

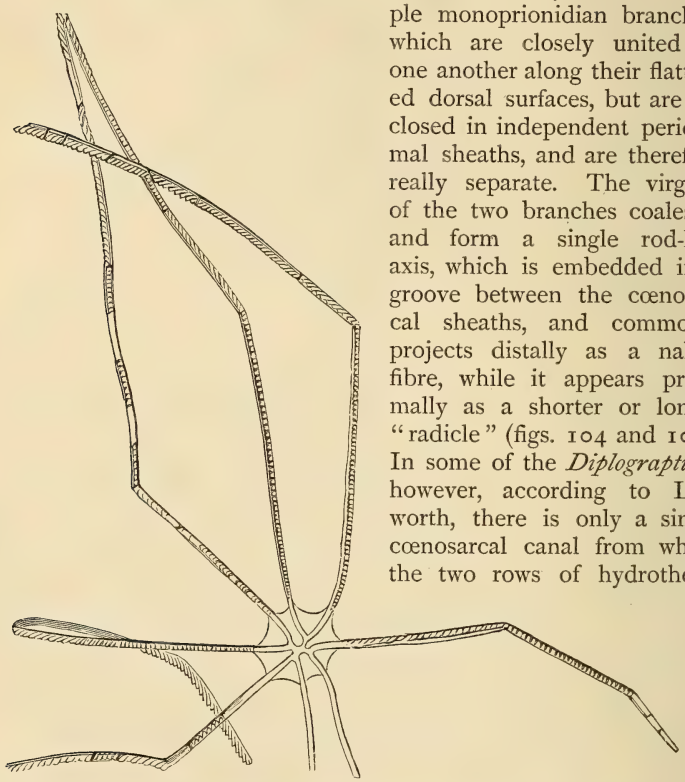

Fig. 102.—*Dichograptus octobrachiatus*, showing the central disc. (After Hall.) Ordovician (Skiddaw and Quebec groups).

spring. The hydrothecæ themselves overlap each other to a greater or less extent, the distal portion of each being free. The species of *Diplograptus* are found in both the Ordovician and Silurian rocks. In the nearly allied genus *Climacograptus* (fig. 105), the structure is much the same as in *Diplograptus*, but the hydrothecæ are vertically disposed, in such a manner that their mouths appear to be sunk below the general surface of the polypary. The appearances present by the polypary in this genus vary extremely, according to

the manner in which the organism has been compressed, or the particular view of the cell-apertures which may be afforded by a given specimen (fig. 105, C, D, E). The species of the genus are all Ordovician and Silurian. Of the remaining genera of the *Diplograptidæ* the only one which needs special notice is the remarkable *Dimorphograptus* (fig. 92, F), in which the proximal portion of the polypary is monoprionidian, while the distal portion is diprionidian. The polypary in its basal part thus resembles a *Monograptus*, which genus it also approaches in the possession of

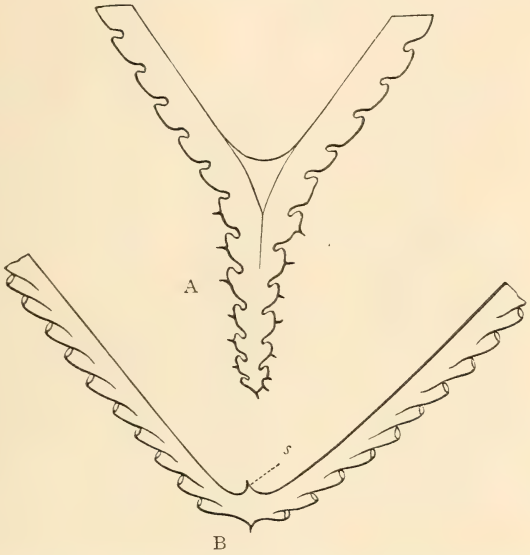

Fig. 103.—A, Proximal portion of the polypary of *Dicranograptus Nicholsoni*, enlarged five times; B, Proximal portion of the polypary of *Dicellograptus complanatus*, enlarged. Ordovician. (After Hopkinson and Lapworth.)

an adherent "sicula"; while in its upper portion it has the characters of an ordinary *Diplograptus*. The known species of *Dimorphograptus* are all Silurian.

Of the remaining families of the Diprionidian Graptolites, the *Lasiograptidæ* are not thoroughly understood, but their distinguishing feature is found in the fact that the biserial polypary is provided with peculiar chitinous spines, arising from the hydrothecæ, which subdivide and inosculate with one another so as to surround the colony with a kind of netted fringe of fine fibres. The type-genus, *Lasiograptus*, is Ordovician. The family of the *Retiolitidæ* is also a peculiar one, the characteristic feature being that the periderm is very much attenuated, and is supported upon a remarkable network

of chitinous fibres, thus producing a minutely latticed appearance of the surface (fig. 106). According to Lapworth, the two virgulæ of the biserial polypary are separated, and are attached to opposite sides of the peridermal network. The type-genus is *Retiolites* itself, the species of which are Ordovician and Silurian. Lastly, the family of the *Phyllograptidæ* includes the single genus *Phyllograptus*, all the species of which are confined to the lower portion of the Ordovician system. In this genus (fig. 107) the polypary is leaf-

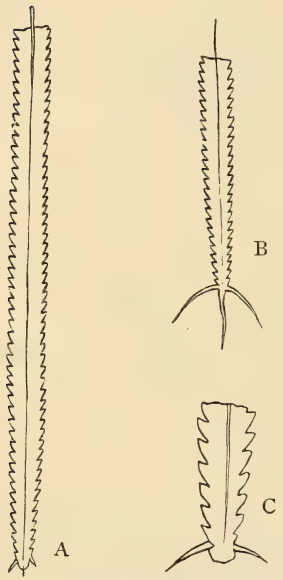

Fig. 104.—A, *Diplograptus foliaceus*, slightly enlarged; B, A *Diplograptus* showing two long lateral spines, in addition to a central "radicle"; C, Base of a *Diplograptus*, enlarged. Ordovician. (Original.)

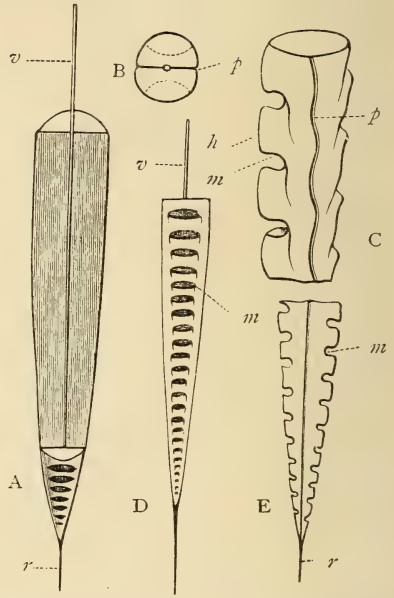

Fig. 105.—A, A specimen of *Climacograptus normalis*, in relief and partially split in half, showing the virgula embedded between the two branches of the duplex polypary; B, Transverse section of the polypary of the same; C, D, and E, Different views of the polypary of the same, showing the appearances produced by differences in the direction of compression. *r*, Radicle; *v*, Virgula; *p*, Septum between the two halves of the polypary; *h*, Hydrotheca; *m*, Aperture. All the figures are enlarged. Silurian. (Original.)

like, and consists of *four* rows of hydrothecæ placed back to back, in such a manner as to resemble two *Diplograpti* intersecting one another at right angles. In consequence of this peculiar structure of the polypary, the *Phyllograpti* are sometimes spoken of as the "tetraprionidian" Graptolites.

The Graptolites have been considered with some detail on account of their great importance in determining the chronological succession

of the Ordovician and Silurian deposits, as has been amply demonstrated by the researches of Lapworth, Linnarsson, and others. Regarded as a whole, the Graptolites, as previously stated, are restricted to the Upper Cambrian, Ordovician, and Silurian rocks, but particular types have been shown to be characteristic of particular horizons in these rock-systems. This is not the place to give an account of the general succession of the *Graptolitoidea* in time, or to indicate the precise stratigraphical value of particular forms of the group, but some general results may be briefly alluded to. The great family of the *Monograptidæ* is wholly confined to the Silurian rocks proper (Upper Silurian of Murchison), the genus *Monograptus*

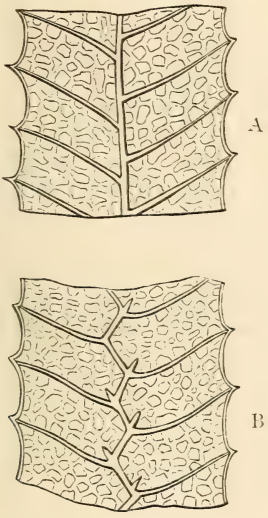

Fig. 106.—Different views of portions of *Retiolites venosus*, enlarged nine times, showing the netted periderm and the virgula. (After Hall.)

Fig. 107.—Group of individuals of *Phyllograptus typus*, from the Quebec group of Canada (after Hall). One of the four rows of cells is hidden on the under surface.

itself extending from the base of this system to its summit. On the other hand, the families of the *Diplograptidæ* and *Retiolitidæ* range from the base of the Ordovician rocks to the middle of the Silurian. The families of the *Leptograptidæ*, *Dicranograptidæ*, *Lasiograptidæ*, and *Phyllograptidæ* are restricted to the Ordovician rocks, and the species of *Phyllograptus*, the sole representative of the last of these families, is only found in the basal beds (Arenig and Llanvirn beds) of the Ordovician. Lastly, the great family of the *Dichograptidæ* commences in the Upper Cambrian period, culminates in the lower Ordovician, and dies out altogether before the commencement of the Silurian. The horizon of the Arenig rocks (Skiddaw and Quebec

groups) is especially characterised by the presence of such genera as *Dichograptus* and *Tetragraptus*, species of these genera being found in rocks of this age in localities as remote as Canada, Britain, and Australia.

Finally, as regards the *zoological affinities* of the Graptolites, palæontologists are now agreed in regarding these singular organisms as an ancient and aberrant type of the *Hydrozoa*. In many respects the Graptolites present a resemblance to the recent Sertularians, this resemblance being shown not only in the fact that the hydrothecæ have a general likeness in form and arrangement in the two groups, but also in the possession by certain of the former of chitinous reproductive capsules, which admit of comparison with the "gonangia" of the latter. On the other hand, the polypary of the Sertularians is always fixed, the hydrothecæ are never in contact, and the colony is not specially strengthened by a horny fibre. In contradistinction, the Graptolites were free organisms, originating in a basal "sicula," the hydrothecæ are usually (but not always) more or less largely in contact, and the polypary is strengthened by the peculiar chitinous rod which has been previously spoken of as the "virgula." In the singular recent genus *Rhabdopleura*, one of the marine *Polyzoa*, the polyzoary is strengthened by a peculiar hollow chitinous axial tube, which has been compared by Professor Allman with the "virgula" of the Graptolites. There are, also, points of resemblance between the Graptolites and those *Polyzoa* (such as *Vesicularia*) in which the cells of the colony communicate by means of a common tube. None of the *Polyzoa*, which possess a chitinous external skeleton, are, however, free and unattached, and the general balance of evidence is unquestionably in favour of a reference of the *Graptolitoidea* to the class of the *Hydrozoa*.

CHAPTER XV.

HYDROZOA — Continued.

HYDROCORALLINES AND STROMATOPOROIDS.

Sub-class Hydrocorallinæ.

The name of *Hydrocorallinæ* has been proposed by Professor Moseley for two groups of marine *Hydrozoa* which produce a regular skeleton of carbonate of lime, and which, on the strength of the skeleton alone, were formerly referred to the true Corals (*Actinozoa*). The two groups in question are the *Milleporidæ* and *Stylasteridæ*, the former being represented by the well-known *Millepora*, which contributes largely to the formation of coral-reefs in various regions. The "cœnosteum" or calcareous skeleton of *Millepora* (fig. 108) is usually in the form of a foliaceous or laminar expansion, or is simply branched, and though minutely spongy, is of considerable density. The main mass of the skeleton is essentially composed of a complex network of anastomosing calcareous fibres, so disposed as to give rise to a correspondingly complex network of anastomosing and tortuous canals (fig. 109, *c c*). In the living condition, this canal-system is filled with anastomosing stolons of the cœnosarc, by which the different zoöids of the colony are placed in organic connection. The general spongy skeleton, constituted as above described, is traversed at intervals by the vertical tubes in which the zoöids were contained. These tubes are in two series, differing slightly in size, and they open on the surface by apertures correspondingly different in dimensions, of which the larger ones are called the "gastropores" and the smaller the "dactylopores" (fig. 108, *g* and *d*). The gastropores and dactylopores may be irregularly distributed, or the dactylopores may be arranged in more or less definite systems round the gastropores. These two sets of tubes, as shown by Moseley, lodge respectively larger and smaller zoöids, which differ in structure and function.

The large zoöids ("gastrozoöids") possess a mouth and digestive cavity, and have from four to six short tentacles. On the other hand, the smaller zoöids ("dactylozoöids") have no mouth, and possess short clavate tentacles on their sides: they are long and slender, and perform the function of prehension for the colony. Whatever may be the structure of the contained zoöids, the zoöidal tubes are intersected internally by distinct transverse calcareous partitions or "tabulæ" (fig. 108, C, and fig. 109, B); but there are no traces of radiating vertical partitions or "septa." The entire cœnosteum shows a more or less evident composition out of thin

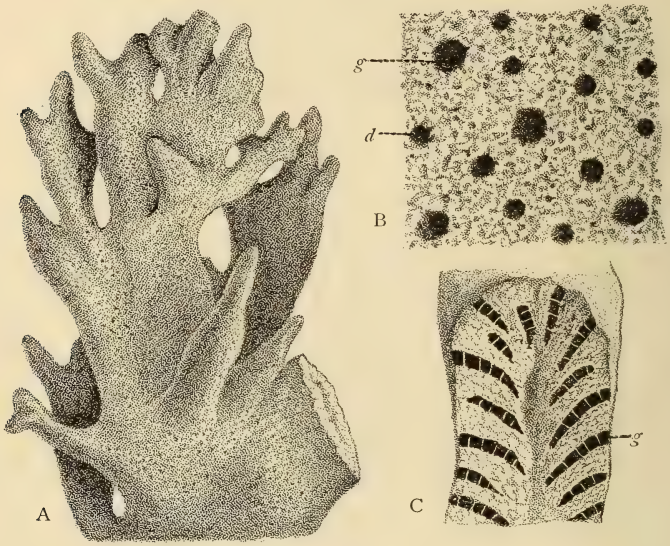

Fig. 108.—A, Portion of the cœnosteum of *Millepora alcicornis*, of the natural size; B, Part of the surface of the same enlarged, showing the mouths of the "gastropores" (*g*) and "dactylopores" (*d*), and the intermediate cœnosteal tissue; C, Vertical section enlarged, showing the tabulate zoöidal tubes. (Original.)

concentric laminæ, only a thin surface-layer being at any given moment actually alive. The reproductive process in *Millepora* is imperfectly known, but Mr Quelch has shown that in one species of the genus the reproductive zoöids are developed within special globular cavities or "ampullæ," which are contained within the general spongy skeleton, and are covered by a thin porous layer.

The structure of *Millepora* has been dwelt upon at some length, as throwing considerable light upon the relationships of the extinct Stromatoporoids, but the genus itself is of little palæontological importance. The earliest known forms of the genus appear in the

Eocene rocks; and in the same formation appears the allied genus *Axopora*, which differs from *Millepora* chiefly in the fact that the tabulate zoöidal tubes are traversed by a large fasciculate "columella" or central rod. The Cretaceous genus *Porosphæra* has been regarded as related to *Millepora*, but it appears to be truly referable to the Sponges.

The second group of the Hydrocorallines is that of the *Stylasteridæ*, comprising a number of recent genera (*Stylaster*, *Allopora*, *Cryptohelia*, *Sporadopora*, &c.), all of which are inhabitants of the sea, and range from the neighbourhood of the coast-line to great depths. The cœnosteum of the Stylasterids is calcareous, more or

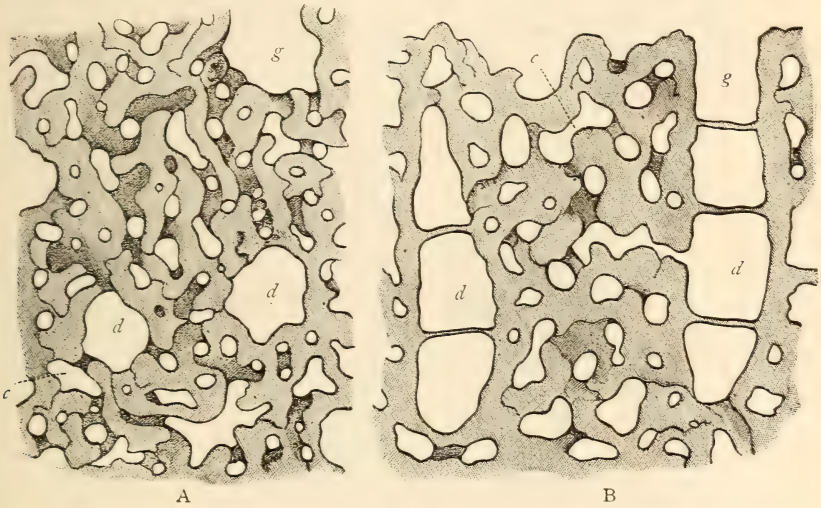

Fig. 109.—Thin sections of *Millepora*, sp., enlarged about thirty-five times. A, Tangential section. B, Vertical section. *g g*, Gastropores; *d d*, Dactylopores; *c c*, Cœnosarcal canals. (Original.)

less branched, forming a dendroid colony or flabellate expansion, and exhibiting upon the surface, or on its sides, small rounded apertures which usually have the appearance of being intersected marginally by radiating partitions or septa, and thus simulate the "calices" of an ordinary Madreporarian Coral (fig. 110). In other cases, the surface shows a series of large apertures, with more numerous and irregularly arranged smaller openings, the latter not being radially arranged round the former. Thin sections of the cœnosteum (fig. 111) show that the general skeleton is composed of a dense, subcrystalline calcareous tissue, which is traversed in all directions by a system of branched and anastomosing canals, which in the living

condition are occupied by prolongations of the cœnosarc, and which place the different zoöids of the colony in direct connection. The zoöids are of two kinds, differing in size, structure, and function. The larger zoöids ("gastrozoöids") are provided with a mouth and stomach-sac; while the others ("dactylozoöids") are elongated and destitute of a mouth, thus coming to represent tentacles in form. The gastrozoöids occupy, as in *Millepora*, the large tubes of the skeleton, and the dactylozoöids are lodged in the small tubes. Hence, when the dactylozoöids are arranged in definite "cyclo-systems" round the gastrozoöids, then each of the large apertures in the skeleton comes to be surrounded by a circle of smaller elongated pores, which are only separated laterally by thin partitions, and which

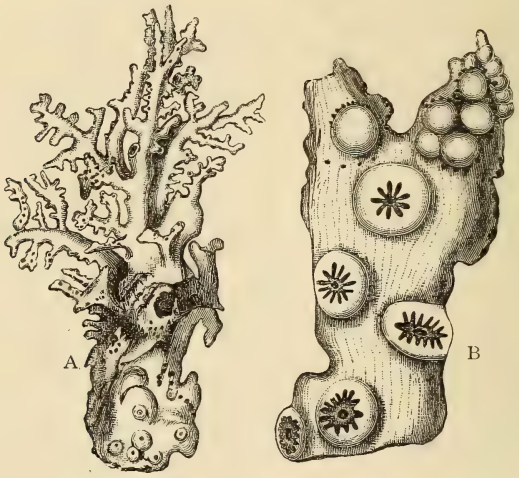

Fig. 110.—A, Portion of the skeleton of *Stylaster sanguineus*, of the natural size; B, Small portion of a branch of the same, enlarged, showing the calices and ampullæ. Living, in the Australian seas. (After Milne-Edwards and Haime.)

thus give rise to the appearance of a central "calice" surrounded by radiated "septa" (fig. 111, c). In certain forms of the Stylasterids, as in *Allopora*, the tubes lodging the gastrozoöids are occupied inferiorly by a reticulate calcareous style or "columella" (a similar structure occasionally existing in the dactylopores); and transverse calcareous partitions or "tabulæ" are sometimes present, though usually in small numbers. Lastly, reproduction in the Stylasterids is effected by means of reproductive zoöids developed within special sac-like cavities or "ampullæ," which at certain periods communicate with the exterior by means of minute pores.

As regards their *distribution in time*, a few species of Stylasterids have been recognised in the Tertiary deposits, the recent genera

Distichopora and *Allopora* being both represented by Tertiary forms. There are also certain Cretaceous fossils, at present imperfectly known, which, according to Moseley, are probably referable to this group. The most ancient allies of the Stylasterids, however, would appear, from the researches of the present writer, to be the singular Triassic fossils for which Professor P. M. Duncan founded the genera

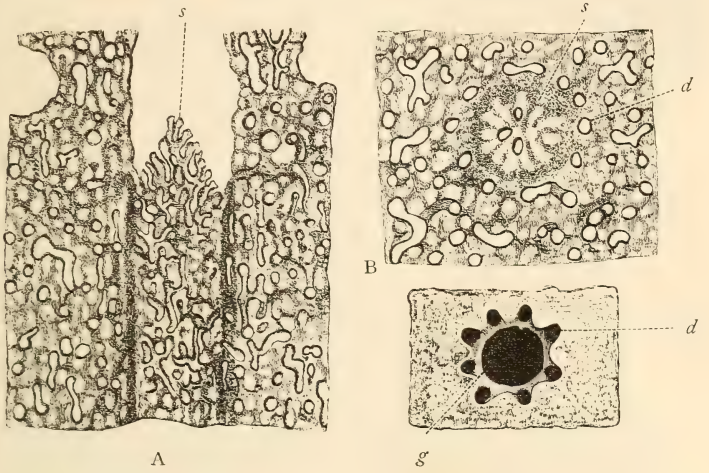

Fig. 111.—A, Vertical section of the cœnosteum of *Allopora*, sp., showing the reticulate cœnosarcal tissue and its canals, greatly enlarged. The section traverses a gastropore, which is seen to be occupied below by a reticulate "columella" (*s*). B, Horizontal section of the same, greatly enlarged, intersecting one of the systems of zoöidal tubes: *s*, Columella of the gastropore cut across; *d*, One of the dactylopores cut across. C, Portion of the surface, enlarged, showing a gastropore (*g*) surrounded by its circle of dactylopores (*d*). (Original.)

Syringosphæra and *Stoliczkaria*.[1] The fossils included in these genera are known as "Karakoram stones," and are found in strata of supposed Triassic age in the Karakoram Mountains, in Kashmir. They are spheroidal or spherical bodies (fig. 112) which vary from an inch or less up to two inches or more in diameter, and which, in unworn specimens, exhibit a warty, verrucose, or granular surface. The surface also generally exhibits rounded pits or pores, which may be uniformly distributed, or which are specially developed along the equatorial diameter of the fossil. There are no traces of any mark of attachment, and the organism must have been free. The

[1] In 1865 Professor Reuss published descriptions and figures of some fossils from the Alpine Trias, for which he proposed the generic name of *Heterastridium* (Sitzungsberichte der Wien Akad. Bd. 51, p. 385, Pls. I.-IV., 1865). It is clear from these that *Heterastridium* is very closely allied to *Stoliczkaria*, if not absolutely identical with it. In case of the identity of these two genera being established, the name of *Stoliczkaria* will have to be abandoned in favour of that of *Heterastridium*, the latter having been published first.

skeleton is calcareous, and its general substance is composed of a characteristic, cancellated or tubulated cœnosarcal tissue, closely resembling the cœnosarcal tissue of *Parkeria*. The tubuli of the general cœnosteal tissue have a radial direction from the centre to the circumference, as in *Parkeria*, but there is no marked arrangement into concentric layers. As seen in cross-sections (fig. 113, A) this tubulated tissue exhibits a characteristic netted appearance. The general cancellated tissue of the skeleton is traversed by numerous comparatively large radiating tubes (fig. 113, *t*), which open on the surface by the rounded apertures above spoken of, and which may be regarded as zoöidal tubes. These tubes, in some cases at any rate, are of differ-

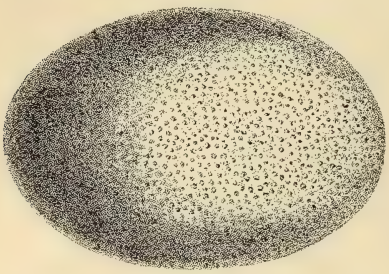

Fig. 112.—A specimen of *Stoliczkaria granulata*, of the natural size, from the Triassic rocks of Kashmir. The surface of the specimen is much worn, but shows the apertures of the zoöidal tubes. (Original.)

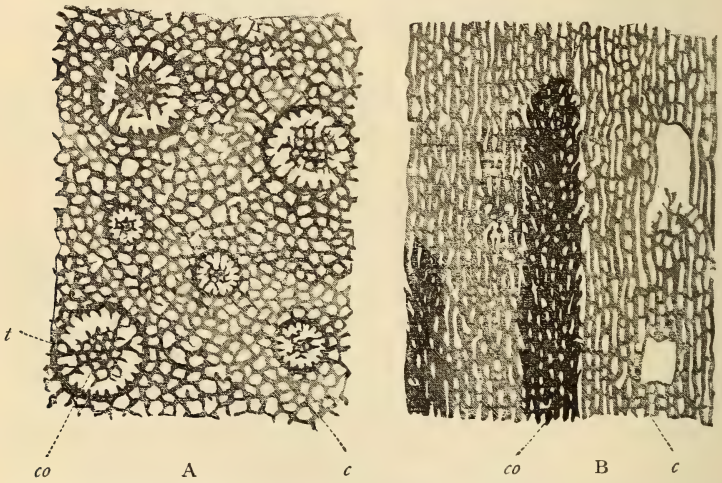

Fig. 113.—Minute structure of *Stoliczkaria*. A, Section of the skeleton taken tangentially to the surface, enlarged twenty-five times, showing the general cancellated cœnosarcal tissue (*c*) and the transversely-divided zoöidal tubes (*t*) with their reticulate columellæ (*co*); B, Vertical section, similarly enlarged, the letters as before. (Original.)

ent sizes, and correspond with the "gastropores" and "dactylopores" of the Stylasterids, and each is provided with a reticulate central style or "columella" (fig. 113, *co*). In cross-sections the

tubes often show the appearance of short inward projections, which have the aspect of the radiating "septa" of a coral, but which are doubtless of a wholly different nature.

The general structure of the skeleton in *Stoliczkaria*, and apparently in *Syringosphæra* also, is thus in many respects similar to that of the recent genera *Allopora* (fig. 111) and *Sporadopora* among the Stylasterids. These singular organisms may therefore be regarded as being referable to the Hydrocorallines, and as being related to the *Stylasteridæ*. From these, however, they differ in their free habit, and in the peculiar radial tubulation of the cœnosarcal tissue; and they may thus be properly considered as constituting a special family, to which the name of *Syringosphæridæ*, proposed by Professor Duncan, may be given. The resemblance between *Stoliczkaria* and *Syringosphæra* on the one hand and *Parkeria* on the other hand, though superficially close, is not dependent on real identity of structure. They agree in the general nature of the cœnosarcal tissue; but the skeleton in *Parkeria* is composed of concentric layers, separated by tiers of chamberlets or by "interlaminar spaces," and is traversed by numerous radial pillars, while the zoöidal tubes are irregular and are devoid of a columellar style.

Sub-class Stromatoporoidea.

The Stromatoporoids constitute a large group of extinct *Hydrozoa*, which, so far as certainly known, are confined to the Ordovician, Silurian, and Devonian rocks. The cœnosteum in the forms included in this group is calcareous and often of large size; and some of the limestones of the Silurian and Devonian period are very largely made up of the skeletons of these organisms. The form of the skeleton and the mode of growth are extremely variable, but the most typical condition of the cœnosteum is that of a spheroidal or irregular mass, or of a flattened expansion, attached basally to some foreign body, and exhibiting a more or less conspicuous composition out of concentric calcareous laminæ (fig. 114). In some cases the skeleton is branched and dendroid, and in others it forms a thin crust growing upon foreign bodies. In this latter case, as well as in some massive types, the organism is attached by the whole of its under surface; but more usually the attachment is by a peduncle, and the greater portion of the basal surface is covered by a thin, concentrically wrinkled, calcareous membrane or "epitheca."

As regards the general structure of the skeleton of the Stromatoporoids, the most obvious feature is that it is composed of numerous concentric layers or "laminæ," which are separated by narrow intervals or "interlaminar spaces." In reality, however, the actually fundamental element in the skeleton is not found in these con-

spicuous concentric laminæ but in a series of vertical calcareous rods ("radial pillars"), which are directed at right angles to the laminæ. The "laminæ," in fact, are not continuous calcareous layers, but are in most cases really formed by numerous irregular calcareous rods or processes which are given out by the "pillars" at definite levels, and which join with one another and with the pillars to form a reticulated or porous membrane. Hence, in a typical Stromatoporoid, the last-formed concentric lamina, which constitutes the outer surface of the organism, exhibits numerous minute pores, which open internally into the uppermost "interlaminar

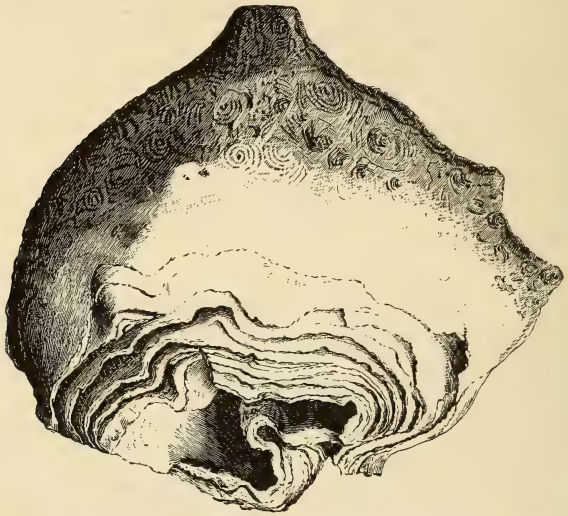

Fig. 114.—A specimen of a Stromatoporoid, of the natural size, showing the concentrically laminated skeleton. The under surface is concave and was probably attached to a foreign body. From the Trenton Limestone of Canada. (After Billings.)

space," and which probably served to give exit to the zoöids of the colony. The outer layer also commonly shows numerous small granules or tubercles, which are really the free upper ends of the vertical or radial pillars. These last-named structures are small calcareous columns, which have a general radial direction, and which cross the interlaminar spaces vertically and thus connect successive concentric laminæ with one another. In some cases (as in the genus *Clathrodictyon*) the pillars are merely short perpendicular processes which run from the upper surface of one lamina to the under surface of the next. In other cases (as in the genus *Actinostroma*, fig. 115, B and C) the pillars run continuously through a considerable number of laminæ. In many cases, it can also be shown

that the radial pillars contain in their interior a minute axial canal (as in *Labechia*, fig. 116, A), but there is no ground for supposing that this opened upon the surface by any aperture.

The zoöids which composed the colony of the Stromatoporoids were sometimes merely lodged in the pores which pierce the reticulated concentric laminæ, and there are no definite "zoöidal tubes" (fig. 115, A). In other cases, such tubes are present; though their recognition is not always easy, and they are often very irregular. When well developed, the zoöidal tubes are usually intersected by

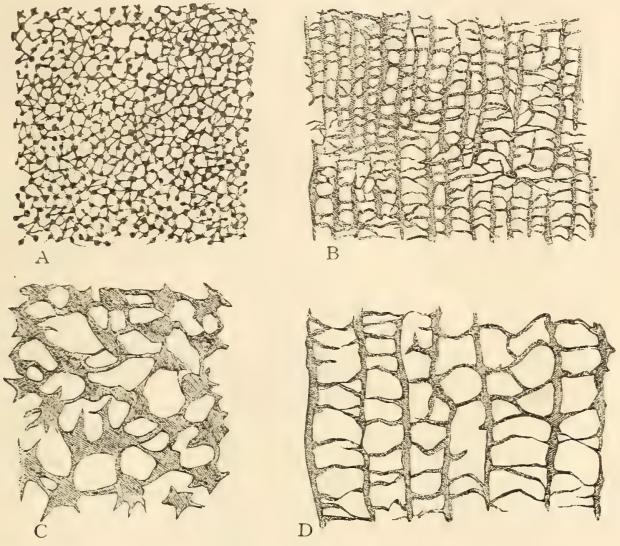

Fig. 115.—A, Tangential section of *Actinostroma intertextum*, showing the transversely-divided radial pillars and the reticulated structure of the concentric laminæ. B, Vertical section of the same, showing the radial pillars and the formation of the concentric laminæ out of processes which are given out horizontally by these. Enlarged twelve times. C and D, Parts of the same sections enlarged further. From the Silurian rocks. (Original.)

a number of transverse calcareous partitions or "tabulæ" (fig. 119, B and D). In no case are the zoöidal tubes provided with radiating vertical partitions comparable with the "septa" of corals. It would seem certain that in all the Stromatoporoids the part of the colony which would be at any given moment actually alive, must have been restricted to a thin external layer.

Among the more noticeable features presented by the Stromatoporoids are the so-called "astrorhizæ" of many types. These are stellate, often much branched, gutters or grooves which are found on the external surface of the last-formed lamina, each stellate system being placed at a little distance from its fellows. As each lamina

of the colony has at one time formed the external surface, the exterior of each exhibits astrorhizæ, as a rule, when the specimen is broken open. Very commonly, also, the astrorhizæ are placed in successive groups one above the other, those of each vertical system being united by a wall-less axial tube, which usually opens on the outer surface by an aperture, which is often placed at the summit of a conical or rounded prominence. The astrorhizal canals of the Stromatoporoids may be compared with the peculiar grooves seen on the external surface of the crusts of the recent *Hydractinia*, or with the branching and inosculating cœnosarcal canals of *Millepora*, and, like the latter, they probably transmitted stolons of the cœnosarc.

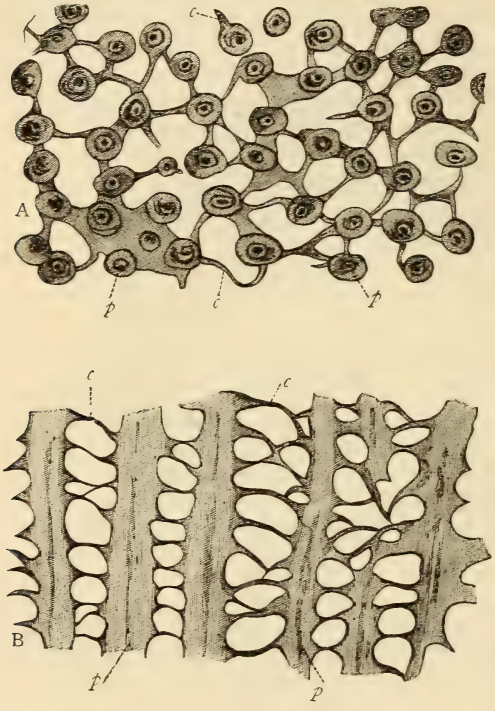

Fig. 116.—A, Tangential section of the cœnosteum of *Labechia conferta*, from the Wenlock Limestone (Silurian), enlarged twelve times. The section shows the transversely divided radial pillars (*p*), with their axial canals, and their connecting processes (*c*). B, Vertical section of the same, similarly enlarged, the letters as before. (Original.)

The Stromatoporoids may be divided into two great groups, the forms of one of these having a resemblance to *Hydractinia* in the structure of the skeleton, while those of the other possess a cœnosteum constructed more nearly after the type of that of *Millepora*. In the first of these primary sections the skeleton (as in *Actinostroma*, fig. 115, and *Labechia*, fig. 116) is composed of "radial pillars" and "concentric laminæ," which remain definitely recognisable and do not become fused with one another into a continuous reticulation. The type of this section is the genus *Actinostroma*, in which the cœnosteum is massive or laminar, often of large size, and the radial pillars are long and are continued without a break through numerous successive laminæ (fig. 115, B). The concentric laminæ

are formed by radiating processes given out in whorls at definite levels from the radial pillars, and uniting with one another in such a way as to give rise to an angular meshwork. Hence, horizontal sections of the species of this genus (fig. 115, A and C) exhibit a structure not at all unlike that of a Hexactinellid Sponge, the cut ends of the radial pillars constituting so many centres from which the horizontal processes forming the laminæ are given out in a stellate manner. The earliest types of *Actinostroma* appear in the Silurian rocks, but the genus is characteristically Devonian. In the nearly allied genus *Clathrodictyon*, the radial pillars are comparatively ill developed, and do not pass from one interlaminar space to another. The species of this genus, though not absolutely unrepresented in the Devonian, are characteristic of the Silurian period.

The singular genus *Labechia* is the type of another group of Stromatoporoids. The cœnosteum in this genus (fig. 117) is usually laminar, attached by a peduncle, and having the under surface covered with a wrinkled calcareous membrane or "epitheca." The upper surface shows no traces of pores or zoöidal apertures, but is covered with numerous blunt tubercles. Vertical sections (fig. 116, B) show that these tubercles are the free upper ends of stout radial pillars, which are connected with one another by numerous arched calcareous plates. Horizontal sections (fig. 116, A) show the cut ends of the radial pillars, united by the calcareous plates above spoken of. The pillars are hollow, with a minute axial canal, but they do not seem to be naturally perforated at their summits. In the absence of definite zoöidal pores, it must be supposed that the surface was covered with the cœnosarc, from which the polypites were budded off. The genus *Labechia* ranges from the Ordovician to the Devonian, and the allied *Rosenella* is found in the Ordovician and Silurian rocks.

Fig. 117.—A small specimen of *Labechia conferta*, from the Silurian rocks of Gotland, of the natural size, showing the epithecate under side and the tuberculate upper surface. (Original.)

In this connection a few words may be here said with regard to the extraordinary and problematical fossils from the Ordovician rocks of North America for which Mr Billings founded the genus *Beatricea*. The fossils in question have the form of cylindrical or angular stems (fig. 118), which are nearly straight, are unbranched, and may attain a length of several feet. The outer surface sometimes shows small rounded tubercles, or may exhibit minute circular apertures, the nature of which is quite uncertain. Transparent transverse and vertical sections (fig. 118, B and C) show that the fossil is principally made up of a thick outer sheath of lenticular calcareous cells

or vesicles, which are arranged in concentric layers round a large axial tube running the whole length of the organism. This axial tube is intersected by strongly curved calcareous partitions or "tabulæ"; and the vesicular tissue which surrounds it is sometimes found to be traversed by columns which radiate outwards to the circumference, and which may be compared with the "radial pillars" of *Labechia*. Upon the whole, with our present knowledge, it would

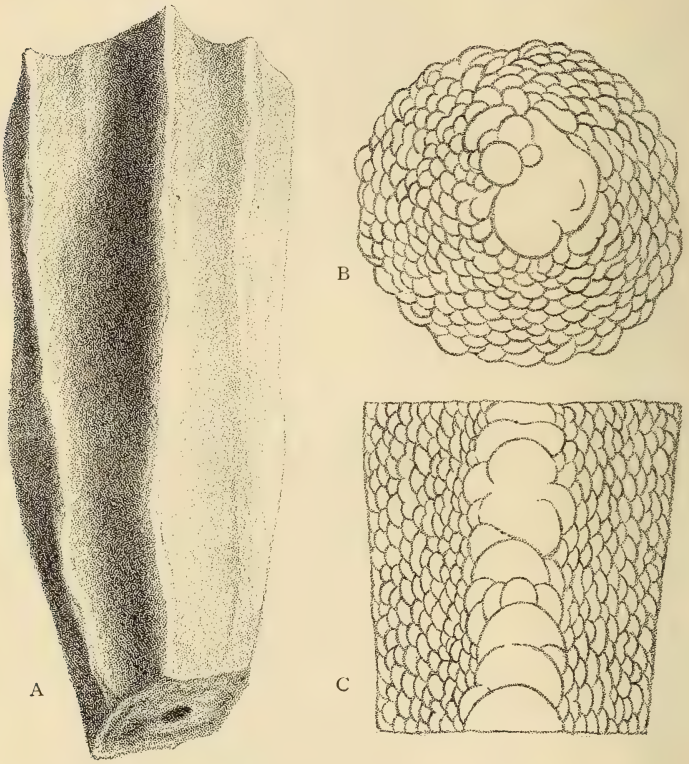

Fig. 118.—A, A fragment of *Beatricea undulata*, slightly less than the natural size, from the Ordovician rocks (Cincinnati Group) of North America. B, Cross-section, and C, Vertical section of *Beatricea nodulosa*, from the same formation, slightly enlarged. The sections show the peripheral vesicular tissue and the central tabulate tube. (Original.)

seem best to regard *Beatricea* as a very abnormal type of the Stromatoporoids, with relationships to *Labechia* and *Idiostroma*; but the position of this anomalous genus must be regarded as more or less doubtful.

The remaining forms of the Stromatoporoids present certain strong resemblances in their structure to the existing genus *Millepora*, and

differ from the types previously considered in the fact that the radial pillars and concentric laminæ are so combined with one another as to lose their distinctness as separate elements, and to become fused with one another so as to form a continuously reticulated skeleton. Moreover, the skeletal tissue has a peculiar microscopic structure, being minutely porous or tubulated (fig. 119, A and B). Definite zoöidal tubes are also present, and these are crossed by more or less

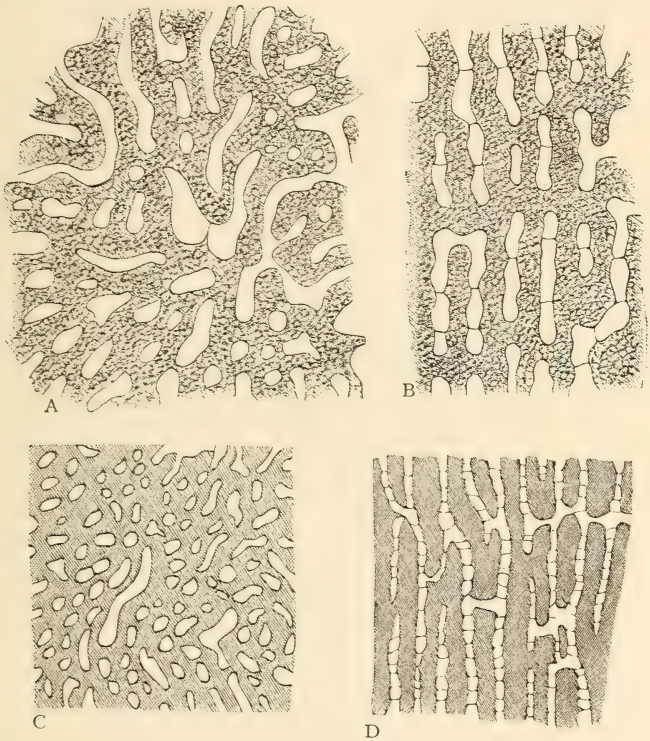

Fig. 119.—A, Tangential section of *Stromatopora Beuthii*, enlarged twelve times, showing the reticulate skeleton and the porous skeleton-fibre; B, Vertical section of the same, similarly enlarged, showing the tabulate zoöidal tubes; C and D, Tangential and vertical sections of *Stromatopora bücheliensis*, similarly enlarged. Middle Devonian. (Original.)

extensively developed transverse partitions or "tabulæ" (fig. 119, B and D). The type of this group is the genus *Stromatopora* itself, in which the cœnosteum is massive or laminar and is usually furnished with an epitheca. The skeleton is completely reticulate, the radial pillars and their connecting-processes being completely fused with one another, so as to give rise to a vermiculate tissue traversed by minute, irregular, tabulate zoöidal tubes. Very commonly, the

massive skeleton is formed of a series of thick concentric strata ("latilaminæ"), each of which is made up of subordinate concentric "laminæ." The type of this genus is the *Stromatopora concentrica* of Goldfuss, a comparatively rare species in the Middle Devonian of Germany and Britain. Upon this species Goldfuss founded the genus *Stromatopora*, but the name has been erroneously given to various Stromatoporoids of quite different affinities. Other species of *Stromatopora* are found in the Silurian and Devonian rocks; and the allied genus *Stromatoporella* appears to be principally if not wholly Devonian.

Lastly, there is a group of Stromatoporoids, represented by genera such as *Idiostroma* and *Amphipora*, in which the skeletal tissue resembles that of *Stromatopora* in its reticulated character, but the cœnosteum is cylindrical and often branched, and is provided internally with a comparatively large axial tube intersected by cross partitions or "tabulæ." The genera above-mentioned are both Devonian, and the sole known species of *Amphipora* (viz., *A. ramosa*) is an abundant and characteristic fossil in the Middle Devonian of Germany and Britain, its slender cylindrical stems occurring in great abundance in particular beds in this formation.

Before leaving the subject of the Stromatoporoids, allusion may be made to the fossils which have been described under the name of *Caunopora*. The fossils in question resemble the ordinary Stromatoporoids, and indeed *are* only Stromatoporoids of various species, with the peculiarity that the general tissue of the cœnosteum is traversed by a number of comparatively large, thick-walled vertical tubes, which open on the surface by definite round apertures. These tubes often spring at the base from horizontal stolons, and are usually connected here and there by lateral tubes of a similar structure to themselves; they usually, if not always, have funnel-shaped, or sometimes horizontal, internal calcareous partitions or "tabulæ," and they occasionally possess rows of short "septal spines." It has been shown that the same species of Stromatoporoid may occur with or without these peculiar "Caunopora-tubes," and there exists further an obvious likeness between these tubes and the corallites of such corals as *Aulopora* and *Syringopora*. Upon the whole, therefore, it may be regarded as probable, if not absolutely certain, that the fossils usually grouped together under the name of "*Caunopora*" are Stromatoporoids which in course of growth have enveloped a colony of some such coral as an *Aulopora* or *Syringopora*, the latter not being thereby killed, but continuing to grow and flourish as a "commensal" within the tissues of the Stromatoporoid.

As regards the *zoological affinities* of the Stromatoporoids, their general structure seems to render it certain that they are referable to the *Hydrozoa*, of which they must be considered to form a special and now unrepresented group. Certain forms (such as *Actinostroma* and *Labechia*) show a decided relationship with the recent *Hydractinia*; while others (such as *Stromatopora* itself) are more closely connected

with the Hydrocorallines, and especially with *Millepora*. These two groups of Stromatoporoids are, however, united by various transitional forms, and they possess structural peculiarities of sufficient importance to preclude the reference of the entire series to any existing division of the *Hydrozoa*.

As to their general *geological distribution*, the Stromatoporoids are not certainly known as occurring out of the Ordovician, Silurian, and Devonian formations. Very few forms have yet been recognised in the Ordovician rocks, but the genus *Labechia* is well represented in strata of this age. The aberrant genus *Beatricea* is also Ordovician. In the Silurian rocks, Stromatoporoids are exceedingly abundant, often entering largely into the composition of the limestones of this period. The predominant Silurian genus is *Clathrodictyon*, but the genera *Actinostroma*, *Stromatopora*, and *Labechia* are also represented. It is, however, in the Devonian rocks, and particularly in the Middle Devonian, that the Stromatoporoids attain their maximum development, the group being represented in strata of this age by numerous species of *Actinostroma*, *Stromatopora*, and *Stromatoporella*, as well as by forms of *Idiostroma*, *Amphipora*, &c. Stromatoporoids have been said to occur in the Carboniferous rocks, but the true nature of these has not as yet been satisfactorily investigated. There are also certain Secondary fossils which, on further examination, may prove to be referable to the present group.

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CHAPTER XVI.

SUB-KINGDOM CŒLENTERATA—continued.

CHARACTERS, STRUCTURE, AND DISTRIBUTION OF THE ACTINOZOA.

THE division of the *Actinozoa* comprises the Sea-anemones, the Corals, and various allied forms, and is defined as including *Cœlenterate animals in which the mouth opens into an œsophageal tube, which in turn opens below into the general cavity of the body* ("*cœlenteric space*"). *The œsophagus is separated from the body-wall by an intervening "perivisceral space," which is divided into a series of compartments by radiating vertical membranous partitions or "mesenteries," to the faces of which the reproductive organs are attached.*

The *Actinozoa* differ, therefore, fundamentally from the *Hydrozoa* in this, that whereas in the latter the space ("cœlenteric" space) included within the body-walls is simple and undivided, and there is no proper alimentary tube, in the former there is a distinct œsophagus (fig. 120, *g*), and the general cavity of the body is divided into radial compartments by vertical membranous plates ("mesenteries").

The tissues of the *Actinozoa* consist of an external "ectoderm" and an internal "endoderm," between which is developed an intermediate layer or "mesoderm" (the "mesoglœa). The ectoderm covers the entire outer surface of the organism, and is prolonged inwards at the mouth to form the lining of the œsophageal tube, while the endoderm lines all the internal cavities of the body. Both the ectoderm and endoderm are primitively cellular, but both are liable to undergo more or less differentiation, muscular fibres, nerve-cells, thread-cells, &c., being developed in process of growth. The mesoderm is essentially composed of connective tissue, and forms an intermediate layer (the "Stütz-lamelle" of the Germans) which gives stability to the soft body of the animal.

The *Actinozoa* may be simple, as in the Sea-anemones, the organ-

ism consisting of a single "polype"; or they may be composite, the organism being composed of more or less numerous polypes connected with one another directly, or united by a common "cœnosarc."

Taking a simple Actinozoön, such as a Sea-anemone (fig. 121), as the type of the class, the body is seen to form a cylindrical tube, the walls of which are formed by the three layers above spoken of, enclosing an internal cavity (the "visceral chamber"). The base of the cylinder is usually completely closed, and often forms a muscular disc of attachment ("pedal disc"). The distal end of the cylindrical body, on the other hand, is perforated centrally by the oval fissure of the mouth, and is furnished round its margin with a series of hollow, muscular and tactile "tentacles." The mouth opens into a membranous œsophageal tube, formed by an infolding of the ectoderm and endoderm, which hangs down into the body-cavity, and terminates at some distance above the proximal extremity of the animal in a wide aperture by which it communicates freely with the general cavity of the "visceral chamber."

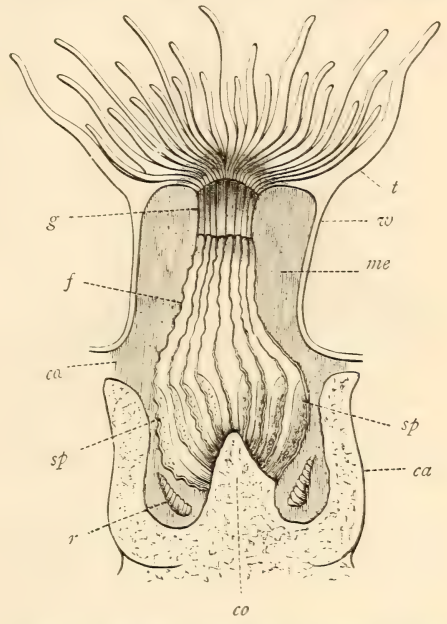


Fig. 120.—A polype of *Astroides calycularis*, a recent Zoantharian, vertically divided. *t*, Tentacles; *g*, Œsophagus; *w*, Body-wall; *me*, Flat face of a mesentery; *f*, Edge of a mesentery; *sp*, One of the calcareous "septa" of the corallum, intervening between the mesenteries; *r*, Reproductive organ; *ca*, Corallum; *co*, Columella; *cœ*, Cœnosarc. (After Lacaze-Duthiers.)

The general space ("visceral cavity") included within the body-walls is subdivided into radiating compartments by a series of vertical membranous partitions, which spring from the body-wall internally and are directed inwards, constituting what are known as the "mesenteries." Some of these partitions—known as the "principal" or "primary" mesenteries—extend all the way from the body-wall to the side of the œsophagus; and in the *Alcyonaria* all the mesenteries do so. In most cases, however, there are shorter mesenteries, which fall short of the gullet, and which are known as

"secondary" and "tertiary" mesenteries according to their relative length. Below the level of the bottom of the œsophagus the inner edges of even the principal mesenteries are free (fig. 120, *f*); and the intermesenteric compartments thus all open freely into a common space, while they may also communicate with one another by means of perforations in their bounding mesenteries, placed near the point where the latter join the upper end of the gullet. Lastly,

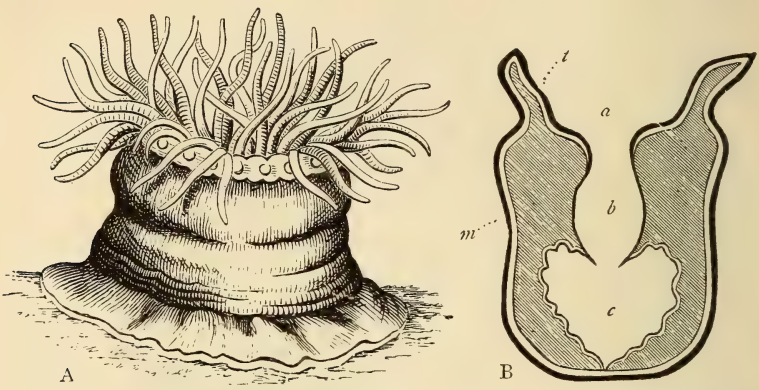


Fig. 121.—A, *Actinia mesembryanthemum*, one of the Sea-anemones (after Johnston); B, section of the same showing the mouth (*a*), the œsophagus (*b*), the body-cavity (*c*), and one of the mesenteries (*m*).

attached to the faces of certain of the mesenteries, towards the lower end of the body, are the band-like reproductive organs (fig. 120, *r*).

As regards the *development* of the mesenteries, Lacaze-Duthiers has shown that in the *Actinidæ* and in *Astroides* the first step is the appearance of a single pair of mesenteries developed at right angles to the oral fissure, nearer to one side than the other, so as to divide the body-cavity into two unequal chambers (fig. 122, 1, 1). In the larger of these chambers appear the two next mesenteries (2, 2), one on each side. Two additional mesenteries (3, 3) next appear in the smaller chamber, this making in all *six* mesenteries; but this condition is evanescent, and two further septa (4, 4) are developed on the opposite side of the first-formed mesenteries to the third pair. At this stage, therefore, there are *eight* mesenteries in all (fig. 122); but two further pairs of mesenteries are produced, raising the number to *twelve*, and completing the series of the "principal" mesenteries.

According, therefore, to the observations of Lacaze-Duthiers, the twelve "principal" mesenteries of *Astroides* are developed in six pairs, which are produced independently and at separate times; and this arrangement seems to hold good in the typical Sea-anemones. The two pairs of "principal" mesenteries which correspond with the opposite extremities of the longitudinal mouth, are known as the "directive" mesenteries. The twelve mesenteries which succeed the twelve "principal"

mesenteries, are developed in pairs in the interspaces between the six pairs of the latter, and additional pairs may be subsequently developed in a similar manner in cycles; but no new mesenteries are produced in the chambers included between the two laminæ which form each pair of "principal" mesenteries.

On the other hand, according to the views of Milne-Edwards and Haime, the mesenteries of the Sea-anemones, and of the ordinary Zoantharian Corals, are developed in a primary cycle of six, to which a second cycle of six is soon added. Should a further development of mesenteries take place, a third cycle of twelve is produced, the new laminæ being formed simultaneously in the intervals between those already in existence; and any further production of mesenteries is

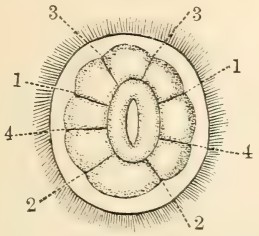


Fig. 122.—Embryo of a Sea-anemone (*Actinia mesembryanthemum*), in which the first eight septa have been developed (after Lacaze-Duthiers). The numerals indicate the order in which primitive septa make their appearance.

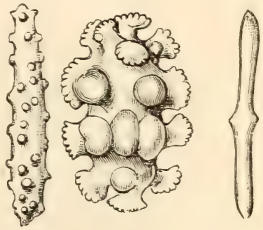


Fig. 123. — Calcareous spicules ("dermosclerites") of the *Gorgonidæ*, greatly enlarged. A, *Gorgonia radula*; B, *Sclerogorgia suberosa*; C, *Melithæa ochracea*. (After Kölliker.)

supposed to take place in obedience to the same general law. So far as the later cycles of septa in the *Hexacoralla* are concerned, the general law has been laid down by von Koch that each new septum is produced in the interspace between two older ones, and the septa of each successive cycle are produced, approximately, simultaneously.

In certain of the *Actinozoa*, such as the Sea-anemones, and the *Ctenophora*, the body remains permanently soft; but most of the animals belonging to this class produce hard structures, which vary much in different cases, and are known by the general name of the "corallum." The simplest form of the corallum is that of detached microscopic "spicules" of carbonate of lime, which are more or less largely developed in the soft tissues, but do not unite with one another to form a coherent skeleton. Such spicules are of common occurrence in the Alcyonarians, and their shape (fig. 123) varies greatly in different types. They are most abundantly developed in the cœnosarc, but may also be present in the walls of the polypes. Though usually permanently separate, the spicules may become so far fused with one another as to give rise to a coherent external skeleton, as occurs in the Organ-pipe Corals (*Tubipora*).

In other cases, as in the Red Coral (*Corallium*), the spicules become fused so as to form a solid cylindrical calcareous axis, which occupies the centre of the cœnosarc (fig. 124). Such a cœnosarcal axis is produced independently of the polypes of the colony, and constitutes what is known as a "sclerobasic" corallum. The form of the sclerobase or axial corallum is simple or branched, in accordance with the undivided or divided condition of the cœnosarc; and its precise structure is very variable. In *Corallium* it is formed of microscopic spicula united by a general calcareous matrix; but in other cases the uniting matrix may be horny, while in the *Anti-*

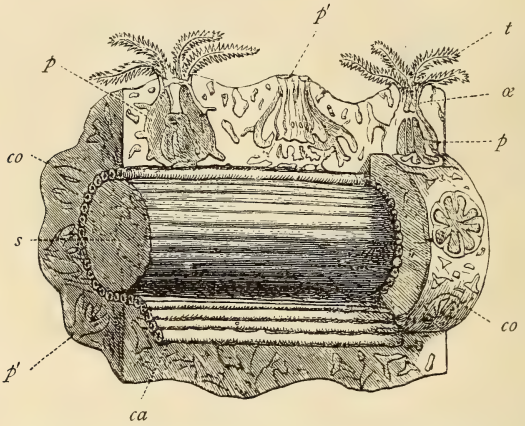


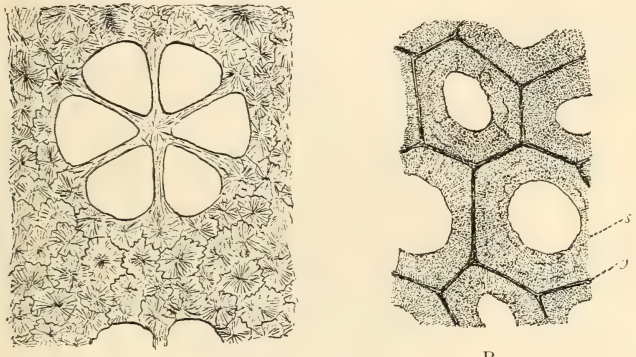
Fig. 124.—A portion of a colony of Red Coral (*Corallium rubrum*), longitudinally divided, and having part of the cœnosarc with its embedded polypes removed. (After Lacaze-Duthiers.) *co*, Cœnosarc, with its embedded polypes, its outer portion traversed by reticulate canals; *s*, Sclerobasic corallum, grooved for the reception of a series of longitudinal cœnosarcal canals (*ca*); *p p*, Polypes having their tentacles (*t*) protruded; *æ*, Gullet; *p' p'*, Polypes retracted within the cœnosarc.

pathidæ and in many of the *Gorgonidæ* the sclerobase is not formed by the fusion of calcareous spicules, but is the result of the secretion of horny matter in successive concentric layers.

In the great majority of the coralligenous *Actinozoa* the corallum is calcareous, and is not formed by the fusion of definite "spicula," but is the result of the secretion of carbonate of lime by the outer surface of the ectoderm. Such a corallum has been commonly spoken of as "sclerodermic." The actual calcareous tissue ("sclerenchyma") which constitutes an ordinary Madreporarian coral has a peculiar microscopic structure, appearing as if formed of bundles of minute calcareous fibres, and commonly having a sub-crystalline character. When these bundles of fibres are cut across transversely (fig. 125, A), they give rise to a characteristic stellate structure, which in some cases (*e.g.*, *Stylophora*, *Pocillopora*, &c.) is of a very regular

nature. In many instances the entire corallum of a Madreporarian consists of the ordinary fibrous sclerenchyma just alluded to. It is not unusual, however, to find that in progress of growth the original skeleton becomes thickened, and its internal cavities more or less restricted, by a deposition of carbonate of lime of secondary origin. This secondarily-formed calcareous tissue has been termed "stereoplasma" by Lindström, and it is often of lighter colour than the sclerenchyma of the original skeleton (fig. 125, B), or is otherwise distinguishable from the latter.

An ordinary sclerodermic coral may consist of a single cuplike structure corresponding with a single polype, or of several such,



A B

Fig. 125.—A, Portion of a tangential section of the corallum of the recent *Stylophora palmata*, enlarged, showing the fibro-crystalline structure of the sclerenchyma. B, A few corallites of *Pachypora Nicholsoni*, Frech, transversely divided and considerably magnified, showing the primordial wall (*v*) and the dense lining of secondary "stereoplasma" (*s*). From the Middle Devonian of Gerolstein. (Original.)

springing directly from one another, or united by a common calcareous tissue ("cœnenchyma") corresponding with the cœnosarc of the colony.

A typical simple sclerodermic corallum (fig. 126) is secreted by a single polype, and its structure presents an obvious correspondence with that of the animal which produces it. It is generally more or less conical in shape, or sometimes discoid, and consists of an outer wall and included space. The wall corresponds with the lower part of the column of the polype, and is known as the "theca." It may be very imperfect, or may be strengthened by a secondary calcareous investment ("epitheca"). The theca encloses a space which corresponds with the lower part of the body-cavity of the polype, and is known as the "visceral chamber." Superiorly the theca terminates in a shallower or deeper, cup-shaped depression, which contains the œsophagus of the polype, and is known as the "calice." Below

the calice, the visceral chamber is subdivided into a number of vertical compartments ("loculi") by a series of upright calcareous partitions or "septa," which spring from the inner surface of the theca, and are directed inwards towards the centre. The septa are calcifications formed within the intermesenteric chambers (fig. 120, *sp*), so that each septum is placed between two mesenteries and underneath a tentacle, and the total number of the septa is equal to that of the mesenteries. The septa likewise increase in number with the increasing growth of the polype, as the mesenteries do; and, like the latter, they vary in their width, so that they are often spoken of as "primary," "secondary," and "tertiary" septa.

The septa of both recent and fossil corals, when examined in cross-sections, commonly show a composition out of two lamellæ of dense,

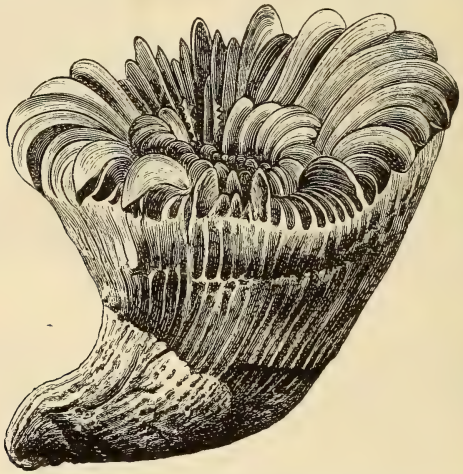


Fig. 126.—*Caryophyllia borealis*. A simple sclerodermic Coral, twice the natural size. (After Sir Wyville Thomson.)

usually light-coloured sclerenchyma ("stereoplasma"), separated by a median, generally dark line (fig. 127).

This central dark line (the "Primärstreif" of the Germans) has been regarded as a mere line of calcification; but it seems to be really a distinct median lamella, representing the primordial septum, while the lateral layers of stereoplasma are of secondary origin. In some cases (as in *Caryophyllia borealis*, fig. 127, A), it appears that this central plate is itself double, and it is probable that it is always so in origin, even though its component elements become completely fused in process of growth.[1] In other cases (as in *Heliophyllum* and its allies), the septa

[1] Hinde has clearly shown that the primary lamella of the septum is really double in the genus *Septastræa*, and a somewhat similar structure of the septa seems to obtain in the recent genus *Flabellum*.

appear to consist principally, or only, of the thin primitive central lamella, no secondary layer of stereoplasma, or but a very imperfect one, being developed. In such cases, the outer wall of the coral is also very thin (fig. 128, B). Where secondary stereoplasma is well developed, the thickened outer ends of the septa usually become fused with one another, so as to form a more or less dense outer investment to the visceral chamber. Sometimes (as in *Streptelasma*, fig. 127, B), the external wall of the corallum seems to be formed wholly by the thickened outer ends of the septa; but in many forms the primitive theca can be recognised in the substance of the outer investment as a thin dark plate (fig. 127, *t*) formed by lateral outgrowths from the primordial septa. Hence in such cases the peripheral ends of the septa continue to grow outwards subse-

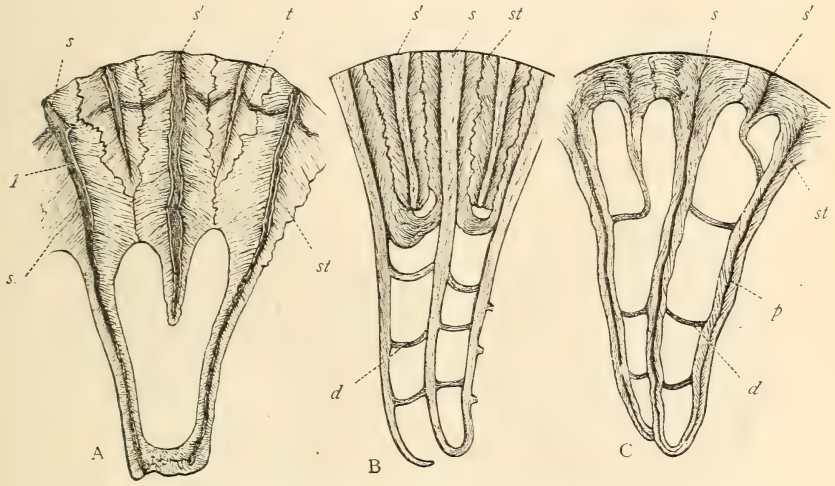


Fig. 127.—A, Portion of a cross-section of the recent *Caryophyllia borealis*, enlarged to show the structure of the septa. B, A similar preparation of *Streptelasma corniculum*, Ordovician, N. America. C, A similar section of *Zaphrentis Enniskilleni*, Carboniferous. *p*, Dark line occupying the middle of the septum; *st*, Layer of stereoplasma; *t*, Theca, formed by out-growths from the outer ends of the septa; *s*, Septum of the first order; *s'*, Septum of the second order; *d*, Dissepiments. (Original.)

quently to the formation of the original theca; each septum thus coming to consist of an intrathecal and an extrathecal portion.

In some corals (as, for example, in *Pholidophyllum*), it can be clearly shown that the septa are made up of calcareous trabeculæ or spines (the "Vertical-leisten" of the Germans), which are directed upwards and inwards towards the axis of the corallum, and which become united with one another directly or by means of secondary sclerenchyma. In *Heliophyllum, Crepidophyllum, Phillipsastræa*, and other allied genera of Palæozoic corals, these oblique septal trabeculæ are greatly developed, and are not obscured by the development of lateral layers of stereoplasma. Hence in these genera cross-sections of the septa (fig. 128, B) exhibit characteristic thickenings or cross-bars, which have been termed "carinæ," and which are the result of the intersection of the septal spines just spoken of, while the free edges of the septa are furnished with pointed projections or teeth.

In many composite corals calcareous structures, as will be subsequently seen, are commonly developed externally to the thecæ of the polypes, constituting what is known by the general name of "peritheca" or "exotheca." In a simple sclerodermic coral, such as we are here considering, the only exothecal structures are the so-called "costæ." These are vertical ridges on the exterior of the corallum, which correspond with the septa, and which, in fact, are the exothecal edges of the septal laminæ. In some cases, however, we meet with similar vertical ridges ("rugæ" or "pseudocostæ") on the exterior of the theca which do not correspond with the septa within, in many instances alternating with the latter; but the true nature of these is not clear. The costæ, when present, vary much as to their relative distance apart, their breadth, their solidity, and their ornamentation with tubercles, granules, or teeth.

In the interior of the corallum various "endothecal" structures may be developed, all of which may be regarded as essentially produced by modifications of, or outgrowths from, the septa. In many

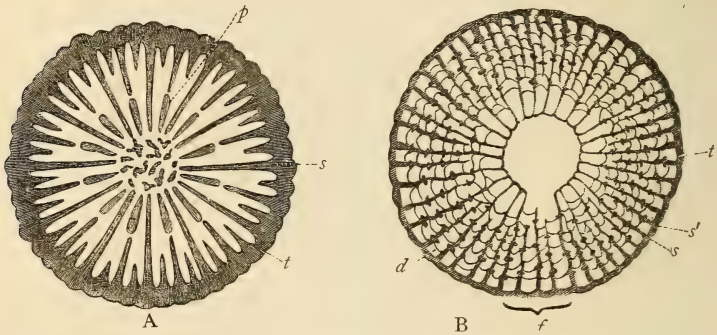


Fig. 128.—A, Transverse section of a simple Zoantharian Coral (*Caryophyllia Bowerbanki*), enlarged. (After Milne-Edwards and Haime.) *t*, Theca; *s*, One of the primary septa; *p*, One of the "pali." In the centre is seen the irregular "columella." B, Transverse section of a Rugose coral (*Crepidophyllum subcæspitosum*), enlarged four times (Original). *t*, Theca; *d*, "Dissepiments"; *s*, One of the first order of septa; *s'*, One of the second order of septa; *f*, "Fossula." In the centre of the coral is a space occupied by tabulæ.

corals the septal laminæ themselves are more or less rudimentary, and may be represented only by vertical rows of spines (as in *Favosites*) or by mere longitudinal striæ (as in species of *Cystiphyllum*). When the septa have the form of complete calcareous lamellæ, they may terminate internally by free edges, and the centre of the visceral chamber may be completely vacant. In other cases, narrow vertical plates which are known as "pali" (fig. 128, A) are developed at the inner ends of certain of the septa, and have the appearance of being continuations of the latter, though detached from them. When a "columella" is present, the inner edges of the pali are united with

this. The "columella" is the general name given to certain axial structures which are commonly developed from the centre of the base of the visceral chamber. The structure of the columella varies in different cases, but it extends, typically, from the floor of the visceral chamber to the bottom of the calice, into which it projects for a greater or less distance; and the principal septa are often more or less closely connected with it. In some cases, the columella is a solid calcareous rod, or it may be made up of reticulated calcareous tissue (fig. 128, A) or of twisted calcareous fibres, while in other instances its structure is even more complicated.

Theoretically, the "interseptal loculi" are vacant spaces or vertical compartments, bounded laterally by the septa, and extending from the lower and lateral surfaces of the theca to the floor of the calice. In practice, however, the continuity of the interseptal loculi is usually more or less interfered with by the development of one or more of the structures known as "synapticula," "dissepiments," and "tabulæ." The "synapticula" are transverse calcareous bars which stretch across the interseptal loculi, perforating the mesenteries, and

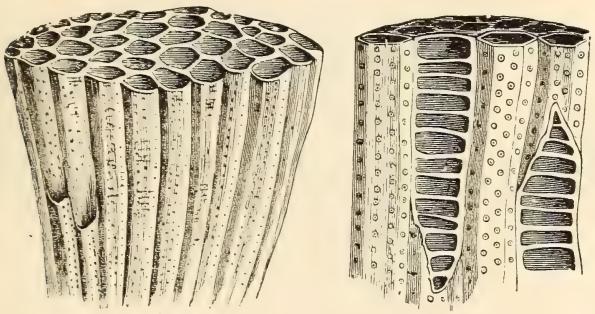


Fig. 129.—A, Portion of the corallum of *Favosites favosa*, of the natural size; B, Portion of four corallites of *Favosites Gothlandica*, enlarged, showing the tabulæ.

form a sort of trellis-work uniting the faces of adjacent septa. They are specially characteristic of the *Fungidæ*. The structures known as "dissepiments" are present in the majority of corals, and have the form of incomplete, oblique or approximately horizontal plates, which stretch between adjacent septa, and break up the interseptal loculi into secondary compartments or cells. Lastly, the "tabulæ" may be regarded as highly developed dissepiments, and, like them, are approximately horizontal, as a rule at any rate. They differ from the dissepiments in the fact that they cut across the interseptal loculi at the same level. When fully developed (fig. 129, B), they are transverse plates, which extend completely across the visceral cham-

ber, and divide it into a series of storeys placed one above the other, the only living portion of the coral being above the last-formed tabulæ. In some cases, the tabulæ are "incomplete," and are merely flat tongue-shaped plates which extend from the inner surface of the theca transversely into the visceral chamber. In other cases (as in *Michelinia*), the tabulæ are imperfect, and become united with one another so as to form a sort of vesicular tissue. In still other cases (as in *Syringopora*) the tabulæ are funnel-shaped, and fit into one another from above downwards.

As regards the process of *development*, the ordinary sclerodermic corallum is the result of the secretion of carbonate of lime by a special layer of ectodermal cells ("calicoblast layer," fig. 130, *ca*), and is therefore truly external to the body of the polype by which it is produced. If the formation of the corallum be observed in the embryo of *Astroides*, it is found that the first step is the secretion of a ring-shaped "basal plate" (fig. 130, *ba*) between the lower surface of the polype and the substance to

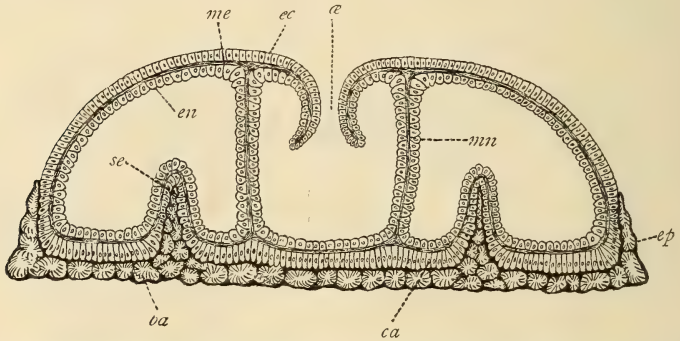


Fig. 130.—Diagrammatic vertical section of a young polype of *Astroides calicularis*, showing the formation of the corallum, greatly enlarged. *ba*, Basal plate, produced by a special layer of ectodermal cells (*ca*); *ep*, Lateral wall of the corallum; *se*, One of the septa, pushing before it a fold of the entire body-wall; *ec*, Ectoderm; *en*, Endoderm; *me*, Mesoderm ("supporting lamella"); *mn*, Mesentery; *œ*, Gullet. (Slightly altered from Bourne, and based on a figure given by von Koch.)

which it has attached itself. The formation of the septa is subsequent to that of the basal plate, these structures appearing as radially-disposed ridges or folds of the base of the polype, each fold (fig. 130, *se*) being composed of the three constituent layers of the body-wall. The septa are thus, like the basal plate, really *external* to the polype; but in process of growth they carry up with them the folds of the body-wall by which they are covered, and they ultimately come to project into the intermesenteric chambers, and to have all the appearance of being internal structures.

The *theca* is not an independent structure, as is the basal plate, but seems to be usually the result of the bifurcation of the peripheral ends of the septa, and the lateral fusion of these (fig. 127, A, *t*). In some cases the external investment of the corallum seems to consist solely of the thickened outer ends of the septa (as in *Streptelasma*, fig. 127, B); but in

other cases there is present, in addition, a secondary calcareous membrane, which is known as the "*epitheca*," and which appears to be secreted by the reflection of the ectoderm over the upper part of the corallum. The "*dissepiments*," which are present in the interseptal loculi of most corals, are secreted by the ectodermal cells ("calicoblasts") of what were "originally the interseptal parts of the base of the polype" (Bourne). The soft parts of the polype thus always lie above the last-formed dissepiments, and the spaces between the latter and the theca are not occupied by soft tissues of any kind.

In connection with the preceding, a few words may be said as to the relations of the polype to the corallum which it secretes. As has been

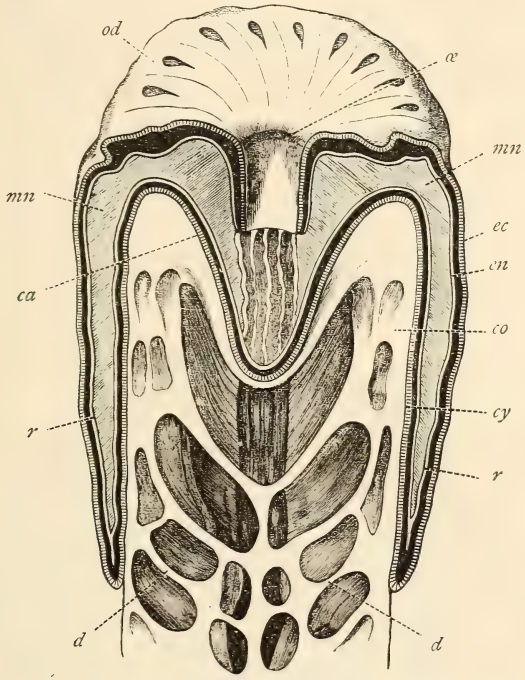


Fig. 131.—Diagrammatic vertical section of *Mussa corymbosa*, showing the relations of the polype to the corallum. *od*, Oral disc of the polype; *œ*, Œsophagus, with the free edges of the mesenteries seen below its inferior end; *mn*, Flat surface of a mesentery; *ec*, Ectoderm (cross-shaded); *en*, Endoderm (unshaded), the dark line between this and the ectoderm representing the mesoderm; *ca*, Special ectodermal layer ("calicoblast layer") secreting the corallum (*co*); *d*, Dissepiments; *r r*, Inversion of the polype constituting the "Randplatte." (Slightly altered from Bourne.)

seen, the corallum is of ectodermal origin, and is therefore really external to the polype. In process of growth, however, the corallum becomes pushed up into the polype from below, so to speak, and thus comes to be apparently situated within the polype. What actually happens, as shown in the accompanying diagram (fig. 131), is that the polype becomes inverted over the corallum, so as to form a layer *external* to the theca, which von Heider has spoken of as the "Randplatte." Thus a portion

of the polype comes to lie *external to the theca*, while a portion lies within the latter. It follows from this that the general body-cavity or "cœlenteric space" is divided by the theca into two parts, of which one is intrathecal, while the other is extrathecal, the latter being divided into chambers by mesenteries, just as the former is. [According to von Koch, the originally continuous mesenteries are cut into two by the fusion of the peripheral ends of the septa to form the theca, each mesentery thus becoming divided into an extrathecal and intrathecal portion.] Above the lip of the calice, the extrathecal and intrathecal portions of the cœlenteric space communicate with one another. It is the extrathecal portion of the polype which forms the "Randplatte" (fig. 131, *r r*); and the so-called "epitheca," when present, seems to be formed "from the free edge of the soft tissues on the exterior of the corallum, as they retreat farther and farther from the original surface of attachment" (Bourne). In composite corals the "cœnosarc" is the result of the coalescence and union of the "Randplatten" of adjacent polypes; and the general calcareous tissue ("cœnenchyma") which unites the various corallites is secreted by the cœnosarc. Where a cœnenchyma is present, the extrathecal portions of the mesenteries are awanting.

The above gives the general structure of a typical simple sclerodermic corallum, as secreted by a single polype. A *compound* sclerodermic corallum is the aggregate skeleton produced by a colony of such polypes, and varies in form and size according to the characters of the colony by which it is produced. In general, such

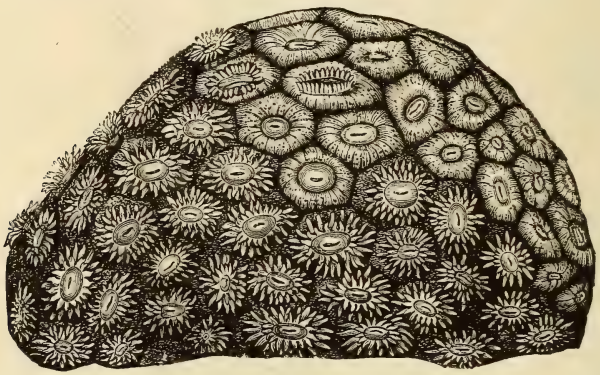


Fig. 132.—*Astræa pallida*, a compound sclerodermic Coral, in its living condition. (After Dana.)

a colony consists (fig. 132) of a number of polypes, which may spring directly from one another, or may be united by a common flesh or cœnosarc; and corresponding elements are found in the corallum. In the former instance, the compound corallum consists of an assemblage of separate "corallites," as the skeletons of the individual polypes are called, these being united with one another directly and in various ways. In the latter instance, the

corallum consists of a number of "corallites" together with a common calcareous basis or tissue, which unites the various corallites into a whole, is secreted by the cœnosarc, and is known as the "cœnenchyma."

The corallites of a composite sclerodermic coral are essentially similar in structure to a simple corallum, such as has been previously described. The "cœnenchyma" is the name given to all those calcareous structures which may unite the different corallites with one another, and which is, therefore, of "exothecal" or "perithecal" origin; and its nature varies greatly in different cases. Most usually, however, the cœnenchyma consists either of simply porous or of compact sclerenchyma; though it may have the form of a reticulated or vesicular tissue. In many of the composite coralla, the corallites composing the colony are also invested inferiorly and laterally by a general calcareous membrane or "epitheca," which is common to the entire growth.

A compound corallum is, of course, primitively simple, and it becomes composite either by budding or by cleavage of the original polype, the following being the principal methods in which this increase is effected.

1. *Lateral or parietal gemmation.*—In this mode of increase the original polype throws out buds from some point on its sides between the base

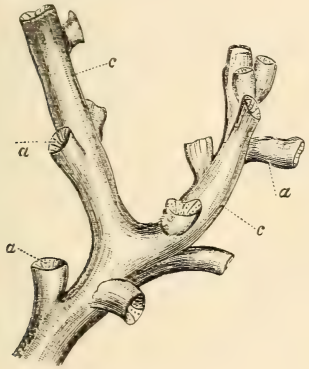


Fig. 133.—A branch of the recent *Dendrophyllia nigrescens* showing lateral gemmation. *a*, A corallite; *c*, Cœnenchyma.

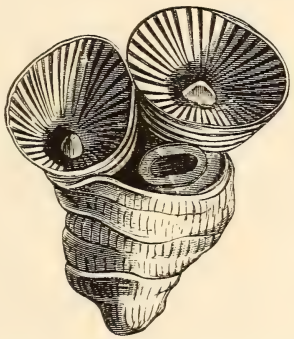


Fig. 134.—Calicular gemmation as seen in *Lonsdaleia floriformis*. Carboniferous.

and the circle of tentacles, and these buds, on becoming perfect corallites, may repeat the process. Commonly the new corallites tend to diverge from one another, the resulting form of corallum being dendroid or branched. In other cases the new corallites grow up side by side, and in contact with one another, the corallum thus becoming massive or "astræiform." Composite corals produced by lateral gemmation may have the corallites directly connected with one another, or united by a more or less copious "cœnenchyma" (fig. 133).

2. *Calicinal or calicular gemmation.*—This consists in the production of buds from the calicine disc of the parent corallite, which may or may not continue to grow thereafter, whilst the new corallites thus produced generally repeat the process. The simplest form of calicular budding is seen in some of the Rugose corals (species of *Cystiphyllum*, *Heliophyllum*, &c.), where the calicine disc gives off but a single bud, which may repeat the process indefinitely, till the corallum presents the appearance of a succession of inverted cones placed one above the other, only the uppermost of these being actually alive. It is not clear, however, that the phenomena here alluded to are really the result of budding, in the proper sense of the term. It is not clear, namely, that the original polype produces a calicine bud which kills its parent; and another explanation of the observed facts would ascribe them rather to a process of "rejuvenescence" on the part of a single polype. On this view, the original polype undergoes periodic contraction and partial death, only the central part of the animal retaining its vitality. Each period of contraction is, however, followed by one of active growth, and the coral thus comes ultimately to assume the form of a succession of inverted cones.

In the more genuine forms of calicular budding, on the other hand, the form of the corallum varies according as the buds spring from the margins or centres of the calices, and as the new corallites remain free or become united with another. In one form of the process, characteristic of certain Palæozoic corals, the original polype throws up from its calicine disc one or more new corallites, which kill the parent. These, in turn, produce others after a similar fashion, till the entire corallum assumes the form of an inverted pyramidal mass resting upon the original budding polype (fig. 134).

3. *Intermural gemmation.*—This mode of budding is seen in the *Favositidæ* and in other extinct corals, and consists in the production of new corallites from the lip of the calicine wall of a pre-existing corallite, instead of from the actual calice itself. Hence in cross-sections of such corals the new corallites appear to be wedged in at the angles of junction of the old corallites (fig. 135, A), and it is not possible to determine from which of the tubes concerned the new bud has been given off. In long sections, again, the new corallite appears as if produced by the splitting of the conjoined wall of two adjacent corallites (fig. 135, B).

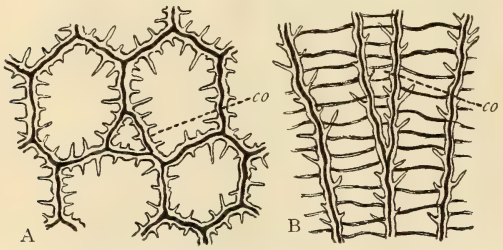


Fig. 135.—Transverse and vertical sections of *Favosites*, enlarged, showing intermural budding. *co*, A young corallite. (Original.)

4. *Basal or stolonal gemmation.*—This mode of increase is specially characteristic of the Alcyonarians, though not confined to these. In this method the original polype sends forth from its base creeping prolongations or "stolons" (fig. 136), from which new corallites are produced. In other cases the same result is attained by the budding of new corallites from a basal laminar expansion. In either case, the youngest corallites are necessarily those nearest to the periphery of the colony.

5. *Fission.*—Fissiparous multiplication commences by the partial

cleavage of the parent polype, the process of division commencing with a constriction of the oral disc, which gradually deepens till the original animal becomes divided into two more or less completely separate polypes, which, however, remain connected proximally. The process is not sharply distinguishable from gemmation, and the form of corallum produced thereby varies greatly in different cases. In many instances the corallites produced by fission may be divided for a considerable distance, remaining connected by the basal portion of the original polype only, the resulting corallum being of a "cæspitose" or tufted form, and consisting of short diverging pairs of branches, of which each pair represents the division of a single corallite. In other cases, the separation of the secondary polypes is very imperfect, and the corallum tends to assume a massive or lamellar form. In such cases the calices form continuous rows, with more or less clearly distinguishable centres, and the calicine furrows are often winding and contorted, as seen in the familiar Brain-corals (*Mæandrina*).

Fig. 136.—*Aulopora serpens*. Devonian.

In such corals as *Chætetes* (fig. 137), the fissiparous development of the new corallites can be generally recognised in sections without

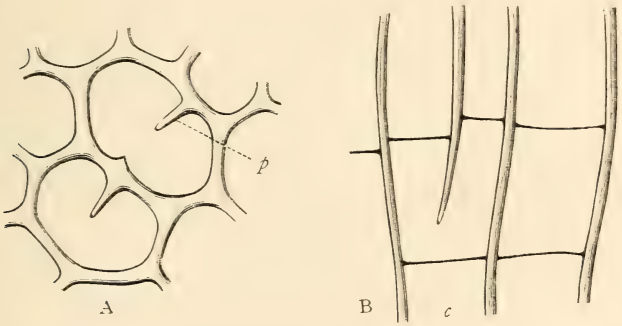


Fig. 137.—Sections of *Chætetes septosus*, from the Carboniferous rocks, enlarged to show fission of the corallites. A, Cross-section of a few corallites, some of which show the commencing fission of a tube by the development of an internal longitudinal partition (*p*); B, Vertical section, showing a single corallite (*c*) splitting into two. (Original.)

difficulty. The commencing fission of a corallite is marked by the development of an internal vertical partition, which is at first incomplete, and which therefore appears in transverse sections as an inwardly directed tooth-like process (fig. 137, A, *p*), looking like a septum. A corresponding partition is then developed opposite to the first one, and by the inward growth and final junction of these, the original tube is ultimately divided into two. In longitudinal sections (fig. 137, B), the fission of a corallite is marked by the appearance of a longitudinal partition in the interior of a tube, which thus becomes divided into two—the two new corallites being at first of small size, but gradually assuming their full dimensions.

As regards the *classification* of the *Actinozoa*, no arrangement that has yet been proposed can be regarded as more than provisional, the true affinities of various important fossil groups being still uncertain. Usually the *Actinozoa* have been divided into the four orders of the *Zoantharia*, *Alcyonaria*, *Ctenophora*, and *Rugosa*. The first three of these divisions are largely represented by living forms, and may be regarded as essentially natural groups; but the division of the *Rugosa* is certainly unnatural, and cannot be retained in its old sense. With our present knowledge—derived wholly from the skeletal structures—it is not possible to speak positively as to the precise relationships of many of the organisms included in the old group of the *Rugosa*. There is no good reason for separating certain of the so-called Rugose Corals from existing groups of the *Zoantharia Aporosa;* but it would not appear to be expedient, in the meanwhile at any rate, to refer the whole of the *Rugosa* to the above-mentioned division of the Madreporarians. The three principal groups of the *Rugosa*—viz., the Cyathophylloids, Zaphrentoids, and Cystiphylloids—are closely connected with one another, and have certain peculiar features of their own. For the reception of these, therefore, it seems to be best, provisionally at any rate, to retain the general name of *Rugosa*, but to regard the forms in question as constituting a special section of the Madreporarians rather than a distinct order.

As regards their general *distribution in space*, all the recent *Actinozoa* are inhabitants of the sea, and there is no reason to suppose that any of the fossil forms were other than marine. The coralligenous forms, generally spoken of as "Corals," are partly inhabitants of deep water, partly shallow-water types; and the latter are well known as giving rise in warm seas, and under suitable conditions, to those great aggregations of coral which are known as "coral-reefs." It is not necessary to consider here the general phenomena of existing coral-reefs, or to enter into a discussion of the vexed question as to the laws and conditions under which the various forms of these structures are produced. A few words may be said, however, as to the nature of the materials which actually form a recent coral-reef, as this is a point which has important geological bearings. In the first place, though Corals properly so called are the principal agents concerned in the construction of a coral-reef, they are not the only ones, a very important part in the formation of the reef being played by other organisms which secrete a calcareous skeleton. Thus, the materials composing a coral-reef are largely the result of the accumulation of the calcareous skeletons of animals other than corals, and particularly of the Hydrocorallines and the Molluscs; while the calcareous *Algæ* (Nullipores) take an important part in the formation of some reefs. Again, it is only a portion—chiefly the outer edge—of a modern coral-reef which is actually composed of living corals,

growing in place; and a large portion of all reefs is formed by calcareous deposits of a fragmental character, which have been produced by the action of the sea upon the reef, and which are therefore essentially made up of larger or smaller pieces of coral mixed with the entire or broken skeletons of other lime-secreting organisms. Lastly, the materials composing a coral-reef are liable to undergo more or less extensive secondary changes caused by the continued percolation through them of water, these changes being in the direction of a more or less complete crystallisation and of a consequent obliteration of the original organic structure of the rock.

Essentially, therefore, a modern coral-reef is composed, on the one hand, of more or less extensive calcareous masses formed by *the growth in place of corals* associated with other lime-secreting organisms, and, on the other hand, of purely mechanical deposits *produced by the wear and tear of the preceding*. As it is known that the reef-building corals do not thrive at depths greater than about thirty fathoms, it is certain that the portions of the reef actually formed of corals which have grown in place must have originated in quite shallow water. On the other hand, the detrital deposits formed by the degradation of the original reef form a belt on the flanks of the latter, and may extend into comparatively deep water. Moreover, the portions of the reef which are of mechanical origin may considerably exceed in amount those which are due to the direct growth of the corals themselves.

The following are the more important kinds of calcareous rocks which occur in existing coral-reefs :—

1. "*Coral-rock*," properly so called, produced by the reef-corals *growing in place*. Though essentially formed by the growing corals themselves, this rock is also largely made up of calcareous mud and the entire or broken skeletons of various lime-producing organisms other than corals, the interstices between the corals being thus completely filled up. This is more especially the case near the surface of the reef, where the branching and reticulated types of corals (such as the Madrepores) chiefly abound. "Coral-rock," produced as above, is liable to undergo secondary changes as the result of the percolation through it of water, the original coralline structure being thus more or less extensively obliterated, and the rock being converted into a compact and crystalline limestone.

2. "*Reef-rock*," produced by the action of the sea upon the reef, and consisting of fragments of broken coral mixed with the entire or broken remains of all sorts of calcareous organisms other than corals (Molluscs, Echinoderms, Foraminifera, Nullipores, &c.), the whole being cemented together by a matrix of crystalline calcite. This matrix is formed by the percolation of water through the mass, this leading to partial solution of the fragments, and to the subsequent deposition in the crystalline form of the carbonate of lime thus obtained. "Reef-rock" is always stratified, and varies in texture, according to the size of the fragments of which it is composed. Usually it is more or less compact and homogeneous; and its component organic fragments may be readily recognisable, or may

be more or less obliterated by secondary crystallisation. In some cases, where the rock is composed of large fragments of coral cemented together by calcareous *débris*, a "coral-breccia" is produced. A somewhat similar rock ("boulder-rock") is formed above the level of high water by the fragments of coral which are heaped up by the waves, and which become ultimately cemented together by the action of the spray.

3. "*Coral-mud*," formed of fine calcareous mud derived from the wear and tear of the reef by the action of the waves. Such deposits are necessarily stratified, and they are more or less fine-grained, chalk-like in appearance, and often friable. Though largely composed of minute particles of carbonate of lime, these coral-muds are often extensively made up of recognisable fragments of various calcareous organisms, or of the minute tests of *Foraminifera*.

4. "*Sand-rock*," formed above high-water mark by the action of the wind. Though subaerial in origin, the "sand-rock" is stratified; and it is composed of fine coral sand cemented together by the action of the spray of the sea, or by the percolation through it of rain-water.

Coralline limestones have been formed in all the great geological periods from the Ordovician onwards, and some of these undoubtedly represent ancient coral-reefs. In an old coral-reef we should expect to find the same two groups of calcareous rocks as have been above noted as occurring in modern reefs. We ought, namely, to meet in a fossil reef, on the one hand, with limestones formed mainly of corals which actually grew in place, and, on the other hand, with limestones produced by the contemporaneous degradation of the reef and therefore made up of the *débris* of corals and other calcareous organisms. Owing, however, to the action of denudation, it must be a matter of comparatively rare occurrence that both these groups of deposits should be found occupying their natural relative positions at the existing surface; and the rarity of such an occurrence must be in direct proportion to the antiquity of the supposed reef. In *any* case, it can only be under exceptional circumstances that the original *form* of any ancient coral-reef can have been so far conserved that it would be possible to determine that the reef was originally a "fringing reef," a "barrier," or an "atoll." In the later Tertiary rocks, no doubt, denudation may have been comparatively speaking so slight that the original form of the reef may admit of determination. Even in the Secondary rocks, however, the changes produced by displacements of the strata and subsequent denudation are so great that the original form of the reefs can hardly be more than a matter of inference. In the still more ancient Palæozoic deposits, again, the dislocations due to earth-movements have been so extensive, and the denudation subsequent to these has been so long continued and so effective, that it must always be hazardous to treat *the existing outcrops of coralline limestones as representing the original boundaries of old coral-reefs*. Hence there is a considerable element of uncertainty attaching to the so-

called "atolls" which have been described as occurring in rocks of Devonian or Carboniferous age. Not only is it theoretically improbable that an "atoll" of such high antiquity as the Devonian should have so far escaped destruction by denudation that its original *form* should still be recognisable, but these supposed atolls are found in areas which can be proved to have undergone extensive disturbance. In such cases, therefore — as, for example, in the "atolls" described by M. Dupont in the Devonian limestones of Belgium — it must be borne in mind that the observed ring-like arrangement of the limestones may well be explained as the result of denudation acting upon a series of strata which contain coralline limestones amongst their members, and which have been folded in a complex manner.

Owing to their peculiar mode of formation, it is clear that those portions of a coral-reef which are formed by corals growing in place must always be terminated by more or less abrupt boundaries; and, for the reasons above given, it is doubtful if the existing outcrops of any of the known Palæozoic limestones can be regarded as actually corresponding with the edges of old reefs. Still it may be permissible to assert that coral-reefs existed in Palæozoic time, provided the term "reef" be used in a wide sense. There are, namely, Palæozoic limestones which are more or less largely composed of corals which grew *in situ*, and these may be looked upon as constituting formations similar to existing coral-reefs, though they are mostly of small thickness, and though their present outcrops must be the result of denudation rather than of original arrangement. On the other hand, very many of the coralline limestones of the Palæozoic period have been only partially, or not at all, produced by corals growing in place, but are essentially of the nature of "reef-rock," being mainly composed of small corals, or of fragments of the larger forms, intermingled with the *débris* of innumerable calcareous organisms of other kinds, such as Crinoids, Brachiopods, Foraminifera, &c. The oldest known coralline limestones occur in the Ordovician period; but still more extensive coralline deposits are found in the Silurian. The corals of these belong principally to the Rugose and Perforate divisions of the *Madreporaria*, but there are also various forms (such as the *Heliolitidæ*) belonging to the *Alcyonaria*. Moreover, these ancient coralline limestones are largely, often preponderatingly, made up of the remains of Stromatoporoids, which are referable to the *Hydrozoa*, or of Monticuliporoids, the precise zoological place of which is not absolutely certain. In the Devonian period we meet with very extensive coralline limestones which, zoologically speaking, are closely allied to those of the Silurian, and in the formation of which the Stromatoporoids again play a very important part. The vast coralline limestones of the Carboniferous period are mostly characterised by the occurrence of Rugose corals (*Lithostrotion*, *Lonsdaleia*, *Cyathophyllum*, &c.), along with Perforate types, such as *Syringopora;* but the Stromatoporoids appear to be now wholly wanting. No true coralline limestones have hitherto been recognised in the Permian rocks; but towards the close of the Triassic period, true coral-reefs were largely developed in Western Europe. Still more extensive reefs were formed during Jurassic times in South-western and Western Europe and in Britain, and true reefs also

existed in Europe during the earlier portions of the Cretaceous period. In the earlier portion of the Tertiary period, again, vast coral-reefs were formed in Central and Southern Europe, in Egypt, Syria, and Arabia, and in parts of India. In the later portions of the Tertiary period, reefs are much more sparingly developed in Europe, but they were at this time formed on a large scale in the warmer regions of the earth's surface. In Mesozoic, Kainozoic, and recent times alike, the chief genera of reef-building corals belong to the families of the *Astræidæ*, *Poritidæ*, and *Madreporidæ*, though the *Oculinidæ* and *Fungidæ* also contribute to the formation of reefs.

With regard, finally, to the *distribution in time* of the *Actinozoa*, the *Ctenophora*, being devoid of hard parts, are unknown in the fossil condition, and need no further consideration here. On the other hand, the *Zoantharia* (including the *Rugosa*) and the *Alcyonaria* are very largely represented in past time, both sections of the class being represented by extinct types in rocks as old as the Ordovician. Speaking generally, the *Actinozoa* of the Palæozoic period belong principally to the Rugose and Aporose divisions of the *Zoantharia* and to certain abnormal groups of the *Alcyonaria*, though the Perforate Zoantharia are by no means unrepresented in rocks of this age. On the other hand, the Mesozoic and Kainozoic periods are characterised by the predominance of the Perforate and Aporose Zoantharians, these being the chief representatives of the class at the present day.

CHAPTER XVII.

CHARACTERS AND DIVISIONS OF THE ZOANTHARIA.

MADREPORARIA APOROSA.

From a palæontological point of view the order *Zoantharia* is not in a satisfactory position, since the only general definition of it which can be given is one based upon the soft parts, and therefore depending mainly upon characters which cannot be recognised in the fossil forms. The living Zoantharians *possess simple, usually numerous tentacles, and the mesenteries are never eight in number.* The mesenteries typically exhibit a more or less clearly recognisable bilateral arrangement, and usually show a hexameral symmetry; but some forms are completely radial, and the disposition of the mesenteries in hexameral cycles is often departed from. In the section of the Rugose Corals, more particularly, the symmetry is typically tetrameral. A corallum may be wholly wanting (*Actiniaria*), or a horny sclerobasis may be developed (*Antipatharia*). In most Zoantharians (*Madreporaria*) there is, however, a well-developed sclerodermic corallum, the symmetry of which varies in accordance with that of the mesenteries.

The general arrangement and structure of the soft and hard parts of the Zoantharians have been sufficiently discussed in dealing with the *Actinozoa* as a whole; but there are some points connected with the symmetry and arrangement of the mesenteries which may be briefly alluded to here:—

Hexameral symmetry obtains as a general rule, though not universally, in the *Actinidæ* (Sea-anemones), *Antipathidæ*, *Madreporaria Perforata*, *M. Fungida*, and *M. Aporosa;* the mesenteries and septa being typically arranged in cycles of six pairs each (fig. 138). On the other hand, tetrameral symmetry is commonly recognisable in the Rugose Corals, though in some of the forms generally in-

cluded in the *Rugosa* a tetrameral arrangement of the septa cannot be clearly made out.

Though showing a *general* radial symmetry, the majority of the Zoantharians at the same time exhibit a distinct bilaterality of their parts. This bilateral symmetry is shown by the presence at each end of the longitudinal gullet (fig. 138, *œ*) of a pair of mesenteries which differ in the arrangement of their muscles from the other mesenteries, and which are known as the "directive" mesenteries. In certain of the Madreporarians (*e.g.*, *Mussa*, *Euphyllia*,

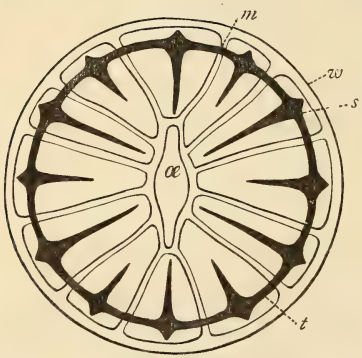


Fig. 138.—Diagram of a cross-section of *Caryophyllia*, the soft parts being unshaded and the corallum black. *œ*, Gullet, with the "directive mesenteries" (*m*) at each end; *w*, Body-wall; *s*, Septum; *t*, Theca. (Slightly altered from von Koch.)

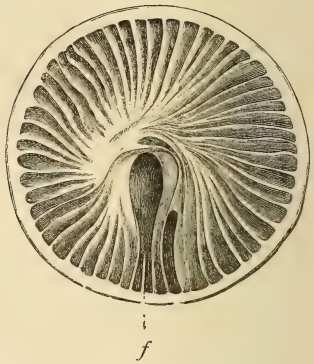


Fig. 139.—Floor of the calice of a typical Rugose Coral (*Zaphrentis Enniskilleni*), of the natural size, showing distinct bilaterality in the disposition of the septa. *f*, The "fossula." From the Carboniferous Limestone. (Original.)

and *Lophohelia*) there are, however, no "directive mesenteries," and in such forms a *complete* radial symmetry obtains. On the other hand, in the typical Rugose Corals very distinct bilateral symmetry usually obtains, and is readily recognised by the general arrangement of the septa, or by an exaggerated or reduced development of certain of these structures. In many Rugose Corals this bilaterality is rendered specially conspicuous by the presence of a shallower or deeper groove or pit—the "fossula"—occupied by a limited number of septa of reduced size (fig. 139, *f*). Sometimes more than one fossula may be present, and the position of the pit thus named varies in different types of the Rugosa, being sometimes dorsal, sometimes ventral, and sometimes lateral.

There seems to be every ground for believing that the "fossula" of the Rugose Corals is connected with the development of the reproductive organs. On this point the observations which have been made by Moseley on the anatomy of the polypes of the recent genus *Seriatopora* are particularly instructive. It has been shown, namely, that in *Seriatopora* it is only two of the twelve mesenteries (viz., the pair of ventro-

lateral mesenteries) which develop reproductive organs. These two mesenteries are much longer than the others, and correspond to intermesenteric pouches of excessive depth, which fit into deep conical pits in the skeleton, bounded by septa of much reduced size. In accordance with these observations, it may be assumed that the "fossula" of the Rugose Corals served to lodge a special hypertrophied mesentery, or group of mesenteries, carrying reproductive organs. It is noteworthy, however, that in the recent *Seriatopora* (as also in *Madrepora Durvillei*) the two mesenteries which are modified for reproductive purposes are *on opposite sides of the polype;* whereas the fossula of the *Rugosa* is usually unilateral.

As regards the *classification* of the *Zoantharia*, the order may be divided into the three groups or sub-orders of the *Actiniaria*, *Antipatharia*, and *Madreporaria*. The first of these comprises the Sea-anemones; and, from the absence of a corallum in these forms, is sometimes spoken of under the name of *Zoantharia malacodermata*. The second group—sometimes called *Zoantharia sclerobasica*—comprises the *Antipathidæ* or "Black Corals" and their allies, in which a horny sclerobase is developed. Lastly, the great series of the Madreporarians — sometimes spoken of as the *Zoantharia sclerodermata*—comprises all the ordinary "Corals" of the present day along with the extinct group of the *Rugosa*, in all of which a well-developed sclerodermic corallum is present.

All the Zoantharians are marine, and from their common possession of a calcareous skeleton they have been largely preserved in the fossil condition. Owing to their want of hard parts, the Sea-anemones (*Actiniaria*) have left no traces of their past existence, and need, therefore, no further consideration here. The group of the *Antipatharia* also requires merely to be mentioned, as no fossil forms have been hitherto identified, the *Leiopathes vetusta* of Milne-Edwards and Haime appearing to be a Gorgonian and therefore referable to the *Alcyonaria*. There remains the great group of the *Madreporaria*, which is represented in past time by a vast series of fossil forms, and which requires, therefore, a somewhat detailed examination.

Madreporaria.

The group of the Madreporarians or *Zoantharia sclerodermata* comprises those Zoantharians in which a well-developed sclerodermic corallum, which is not simply spicular, is present. The septa of the corallum are, typically, arranged according to either a hexameral or a tetrameral system; but in some cases some other numerical law may govern the disposition of the septa, and in other cases no special symmetry may be recognisable. The organism may be simple, consisting of a single polype only, or composite, consisting of many

polypes united with one another directly, or connected by a general cœnosarc.

A strictly natural classification of the *Madreporaria* has still to be framed. By Milne-Edwards and Haime they were divided into the four sections of the *Aporosa*, *Perforata*, *Tabulata*, and *Tubulosa;* while these authorities considered the *Rugosa* as a distinct order. The section of the *Tabulata* ("Tabulate Corals") has, however, been shown to be a miscellaneous and artificial assemblage, and the types formerly included in it have now found a place in the Aporose or Perforate sections of the order, or have been relegated to the *Alcyonaria*. The section of the *Tubulosa*, again, is a small and imperfectly understood one, and the forms included in it may be temporarily placed in the *Alcyonaria*. Lastly, recent researches and discoveries have rendered hardly tenable the retention of the *Rugosa* as a separate order of *Actinozoa;* though the true affinities of many of the so-called Rugose Corals are still very uncertain. In the present state of our knowledge, the *Madreporaria* may be divided into the four primary sections of the *Aporosa*, *Rugosa*, *Fungida*, and *Perforata*. Of these, the *Fungida* do not appear to have come into existence prior to the Jurassic period; but the remaining three sections were differentiated as early as the Ordovician period.

Section I. Madreporaria Aporosa.

The division of the *Aporosa* comprises those Madreporarians in which the corallum is composed of more or less compact and solid sclerenchyma, the "theca" or wall surrounding the visceral chamber being *complete*, and not perforated by apertures or pores (fig. 140). An "epitheca" may be present. The septa are well developed, and usually have the form of solid lamellæ, though they are in some cases more or less cribriform. The interseptal loculi may be open throughout, but endothecal tissue in the form of "dissepiments" is usually more or less largely developed, while "synapticula" and "tabulæ" are sometimes present. The corallum may be simple or composite. The symmetry may be completely radial (*Mussa* and *Euphyllia*), or bilateral. The arrangement of the septa is typically hexameral, but may be tetrameral, pentameral, or otherwise abnormal.

It is difficult to speak positively as to the *geological distribution* of the *Madreporaria Aporosa*, owing to the uncertainty which attaches to the precise affinities of many fossil Corals. There are, however, various Palæozoic types which may most suitably find a place here, the Ordovician genus *Columnaria* (*Favistella*) being apparently the most ancient of these. The Silurian genus *Stauria*, in spite of its tetrameral symmetry, may likewise be regarded as an Astræid; while *Duncanella* and *Cyathaxonia*, the former Silurian and the latter Car-

boniferous, may be looked upon as early types of the *Turbinolidæ*, as, perhaps, *Petraia* and *Polycœlia* may also be. Professor Duncan further regards the Devonian genus *Battersbyia* and the Carboniferous *Heterophyllia* as representing a special group of *Aporosa* allied to the *Astræidæ*. In the Secondary and Tertiary deposits the Aporose

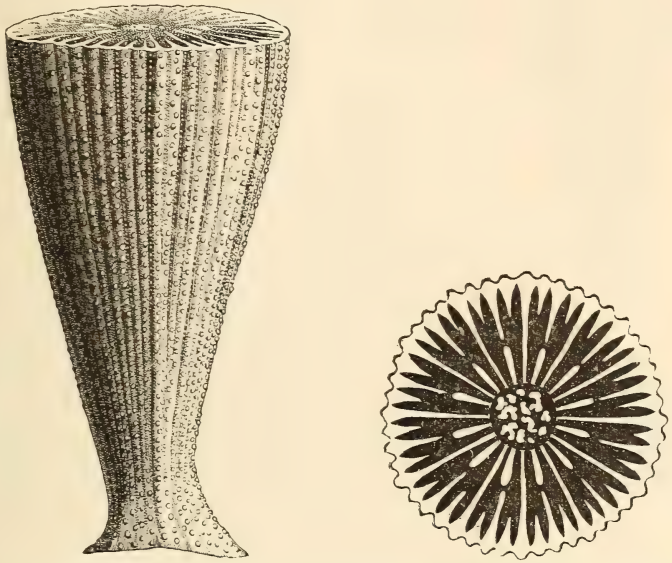


Fig. 140.—*Caryophyllia* (*Cyathina*) *Bowerbanki*, from the Gault (Cretaceous). The left-hand figure represents a specimen imperfect above, and enlarged, showing the tuberculated costæ. The right-hand figure is a magnified cross-section, showing the septa and pali. (After Milne-Edwards and Haime.)

Madreporarians are represented by a vast number of types, which do not essentially differ in plan of structure from existing forms.

The *Madreporaria Aporosa* are divided into the following families :—

Family 1. *Turbinolidæ*.—In this family the corallum is generally simple, or when compound is destitute of a cœnenchyma. The wall is solid and imperforate, and the septa are in the form of lamellæ, often granulated on their sides. The *interseptal loculi are open from top to bottom*, no endothecal structures in the form of dissepiments or synapticulæ being developed. A few Palæozoic Corals (such as *Duncanella* and *Cyathaxonia*) may be referred here, but the family is mainly Secondary and Tertiary.

The number of forms included in the *Turbinolidæ* is so large, that only a few of the leading types of the family can be here referred to in the

briefest way. In the genus *Turbinolia* itself (fig. 141), the corallum is simple and conical, with a projecting styliform columella, but without pali. The costæ are very prominent, and the spaces between them are marked with rows of small dimples, which look like perforations in the wall, but do not really penetrate to the visceral chamber. The genus is well represented in the Lower Tertiary deposits, but is doubtfully recent. In *Smilotrochus* and its allies there is no columella, and pali are rarely present. The type-genus is Cretaceous and Tertiary. The genus *Flabellum* is the type of another group of the family, and is distinguished by the compressed and wedge-shaped form of the corallum, the calice thus assuming an oval form. The structure of the wall and septa in *Flabellum* is peculiar, but is not so different from that of the same parts in certain fossil corals of other groups as to justify the removal of the genus from its present position. The species of *Flabellum* are all Tertiary and Recent. In *Placotrochus* and its allies a columella of a lamellar form is present, and there are rarely pali. The genus is Recent and Tertiary, as also is the related genus *Sphenotrochus*. The genus *Trochocyathus* is the type of an extensive series of forms, in which there is a fasciculate columella, and generally one or more cycles of pali. *Trochocyathus* itself (including *Thecocyathus*) dates from the Lias, and ranges to the present day. Allied to this is the well-known genus *Caryophyllia* (figs. 140 and 126), which ranges from the Cretaceous period to the present day, and is distinguished by its possession of a trabecular columella and a single crown of pali (fig. 128, A).

Fig. 141.—*Turbinolia sulcata*. The upper figure shows the exterior of the theca with the costæ. The lower figure shows the calice, with the columella and primary and secondary septa. Eocene.

The remaining types included in the *Turbinolidæ* are more or less abnormal. The genus *Dasmia*, for example, is so peculiar, that it has been regarded as the type of a separate family (*Pseudoturbinolidæ*), the distinctive feature being that the septa are arranged in groups of three, in such a way that each septum might be regarded as formed by the coalescence of three elements. The genus is Cretaceous and Tertiary. The Recent genera *Guynia* and *Haplophyllia*, again, are remarkable in the fact that the symmetry of the corallum is tetrameral, and they thus serve to lead us to such ancient types as the *Cyathaxoniæ* of the Carboniferous rocks. In the true *Cyathaxoniæ* (as typified by the *Cyathaxonia cornu* of the Mountain Limestone) the corallum is simple and conical, the septa having a tetrameral symmetry, and a "fossula" being present. There is a prominent columella, and the interseptal loculi appear to be free from endothecal structures. As the presence of a fossula, and the fact that the septa have a tetrameral arrangement, cannot be considered as distinctive features, there would not appear to be sufficient ground for excluding this genus from the *Aporosa*. The Silurian corals which have been included in the genus *Cyathaxonia* belong, however, to the genus *Lindstrœmia*, which may also be referable to this division of the *Madreporaria*, though it will be here provisionally placed among the *Rugosa*.

Another Palæozoic type that may with great probability be included among the *Turbinolidæ*, is the Silurian genus *Duncanella*. In this genus (fig. 142) the corallum is simple and conical, with a deep calice, and a well-developed wall marked by costæ and encircling striæ. The wall, however, is deficient at the extreme base of the corallum, thus allowing the primitive septa to protude as a little cone (fig. 142, B). There are eighteen (sometimes seventeen) septa, the symmetry of which is completely radial, and which meet centrally so as to form a sort of pseudocolumella (fig. 142, C). The interseptal loculi, as in the *Turbinolidæ* generally, are completely open, and are free from endothecal structures of any kind, though the bottom of the visceral chamber is more or less extensively filled up by a deposit of stereoplasma.

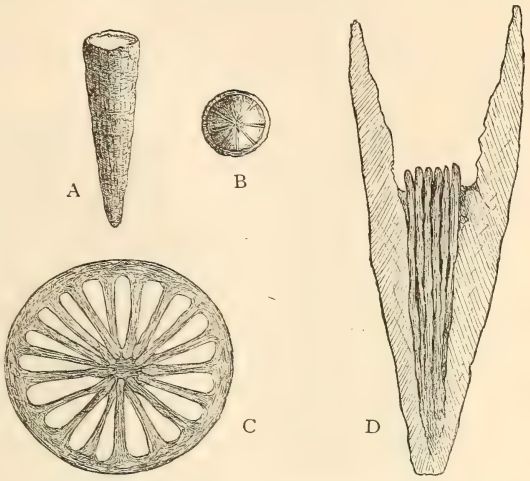


Fig. 142.—*Duncanella borealis*, from the Silurian of North America. A, Side-view of the corallum, enlarged twice; B, Base of the corallum, enlarged, showing the absence of the wall and the protrusion of the septa; C, Transverse section of the corallum, enlarged nine times; D, Vertical section of the corallum, enlarged four times. (Original.)

Lastly, it is probable that the imperfectly understood genera *Petraia* and *Polycœlia*, both of which are of Palæozoic age, may ultimately be shown to be aberrant types of the *Turbinolidæ*.

Family 2. *Oculinidæ*.—The corallum in this family is always composite (fig. 143), the new corallites being usually produced by lateral gemmation, and being united by an abundant and compact cœnenchyma, the surface of which is smooth or striated, but is not echinulate. The wall of the corallites is imperforate, not distinct from the cœnenchyma, and the lower portion of the visceral chamber usually becomes extensively filled up in process of growth by a deposition of stereoplasma. The interseptal loculi are usually open to the base, but dissepiments or (as in *Lophohelia*) tabulæ are occasionally developed.

The *Oculinidæ* appear for the first time in the Jurassic rocks (*Euhelia*, *Enallohelia*, &c.), and are also represented in the Cretaceous rocks (*Synhelia*, fig. 143, *Diblasus*, *Baryhelia*, &c.) In the Eocene Tertiary we meet with early types of the Recent genus *Oculina* itself, with its arborescent corallum and nearly smooth cœnenchyma. The well-known living genera *Amphihelia* and

Lophohelia likewise appear in the Tertiaries, the former in the Eocene and the latter in the Miocene. Lastly, the widely distributed Recent genus *Stylophora* (fig. 144) appears as early as the Eocene Tertiary. The corallum in this genus is readily recognised by its granulated cœnenchyma, the presence of a styliform columella,

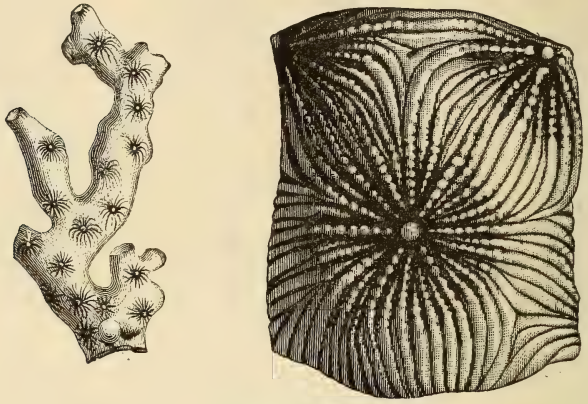


Fig. 143.—*Synhelia Sharpeana.* Cretaceous.

and the fact that there are six fully-developed septa, with an intermediate cycle of six rudimentary septa.

Family 3. *Pocilloporidæ.*—The corallum in this family is composite, with a dense cœnenchyma, the corallites having their visceral chambers largely filled up inferiorly with solid stereoplasma (fig. 145, c). The calices are oval, and are definitely oriented, their long axes corresponding with that of the branches of the corallum. The septa are small, twelve in number, with a distinct bilateral arrangement. The cavities of the polypes are placed in communication (as in the Alcyonarians) by a network of canals, which traverse the superficial region of the colony. The mesenteries of the ventro-lateral pair are, moreover, much longer than the others, and are the only ones which carry mesenterial filaments, and which develop reproductive organs. In *Seriatopora*, as shown by Moseley, these two mesen-

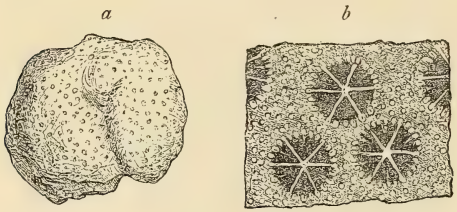


Fig. 144.—*a*, The corallum of *Stylophora subreticulata*, from the Miocene Tertiary of Austria, of the natural size; *b*, Surface of the same, enlarged. (After Zittel.)

teries correspond with especially deep intermesenteric pouches, which fit into deep pits in the floor of the visceral chamber. These pits are bounded by septa of much reduced size, and may be fairly compared with the "fossula" of the *Rugosa*.

This family comprises only the two genera *Pocillopora* and *Seriatopora*, both of which, as above shown, have certain very remarkable characters, and make a decided approach to the Rugose Corals. In *Pocillopora* (fig. 145), there is a small columella, and well-developed

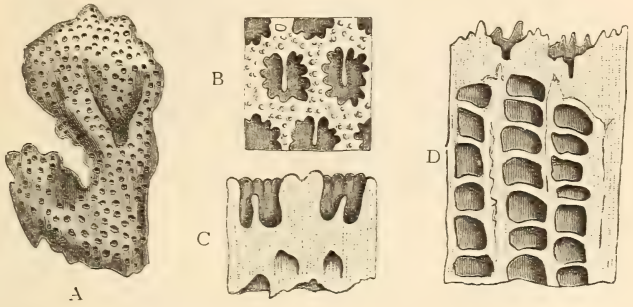


Fig. 145.—A, Portion of the corallum of *Pocillopora aspera*, var. *lata*, Verrill, of the natural size; B, Part of the surface of same, enlarged; C, Section of the corallites of the same, showing the columella, enlarged; D, Vertical section of the same, enlarged, showing tabulæ. (After Dana.)

tabulæ (fig. 145, D) are present. The genus ranges from the Miocene Tertiary. In *Seriatopora*, on the other hand, there is a large compact columella, and only traces of tabulæ are present. No fossil forms of this genus have been hitherto discovered.

Family 4. *Astræidæ*.—In this large family of the *Aporosa* the corallum may be simple or composite. Endothecal tissue in the form of dissepiments is well developed, and tabulæ are present in some forms. The septa are lamellar, their free edges being sometimes smooth or entire, sometimes dentated or ragged. The increase of the composite coralla (fig. 146) is effected by gemmation or by fission, and the new corallites usually become united directly by their walls or costæ, or in other cases by vesicular exothecal tissue, a solid cœnenchyma being rarely developed.

If *Columnaria* be admitted into the *Astræidæ*, the family is represented as early as the Ordovician period. The Silurian genera *Stauria* and *Acervularia* (as typified by *A. ananas*), the Devonian *Battersbyia*, and the Carboniferous *Heterophyllia* may likewise be regarded as Palæozoic types of the *Astræidæ*, though all depart in different respects from the ordinary forms of this family. Leaving the Palæozoic period, we find a great development of *Astræidæ* to take place towards the close of the Trias, where the

family is represented by numerous and varied types; a still further expansion takes place in the Oolites; very numerous forms are met with in the Cretaceous, and though there is some

Fig. 146.—*Thecosmilia annularis.* Coral-rag, England.

decrease in the Tertiaries, this great family still holds its ground as the most important group of the "reef-building" corals.

The family of the *Astræidæ* admits of subdivision into a number of minor groups, and comprises such a vast number of forms that it is impossible to do more here than to allude to a few of the more important types. In the first place, there is a large series of forms (*Astræa simplices*) in which the corallum is simple and solitary. These simple Astræans appear under many generic types in the Secondary period, and have survived to the present day. Well-known genera are *Montlivaltia* (fig. 147), ranging from the Trias to the Recent period; *Trochosmilia*, ranging from the Jurassic to the Miocene; and *Parasmilia*, ranging from the Cretaceous to the present day.

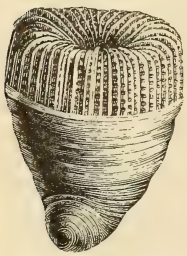


Fig. 147.—*Montlivaltia caryophyllata*, showing the greatly-developed epitheca covering the lower part of the coral. Great Oolite.

In a second group of the Astræans (*Astræa reptantes*), comprising such genera as *Rhizangia* and *Astrangia*, the corallum is composite, and consists of short corallites budded out from basal stolons or expansions. *Rhizangia* is Cretaceous and Tertiary, while *Astrangia* is represented in the Eocene Tertiary, and survives at the present day.

In a third group of Astræans (*Astræa gemmantes*) are comprised compound forms, in which the mode of increase is "by gemmation from the wall below the calicular margin" (Martin Duncan). In this group are included various Secondary, Tertiary, and Recent corals (*Cladocora*, &c.), and Professor Martin Duncan also places here the remarkable

Palæozoic genera *Heterophyllia* and *Battersbyia*. In the former of these (fig. 148) the corallites are long and slender, increasing by budding around the calicular margin. There is a thick wall, marked by prominent costæ, which may be variously ornamented. There may be only six septa; but there is usually a larger number of these structures, their

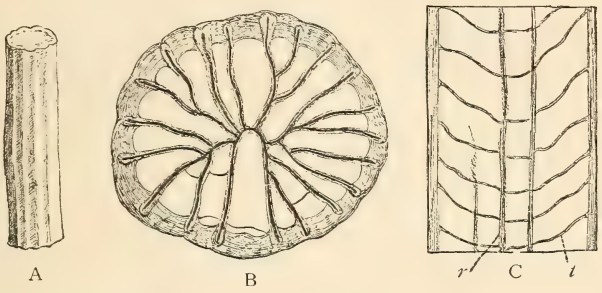


Fig. 148.—*Heterophyllia angulata*, from the Carboniferous Limestone of Northumberland. A, A fragment of the corallum, enlarged slightly. B, Transverse section of the same, enlarged seven times. C, Longitudinal section, similarly enlarged: *t* Tabulæ; *r* Cut edges of the septa. (Original.)

arrangement being distinctly bilateral, and in many respects resembling that seen in young examples of *Zaphrentis*. Some of the septa usually became coalescent, so as to give rise to fan-like groups, while the longer septa are continued to meet in the centre of the visceral chamber. There is no true columella, but a "fossula" is often present (fig. 148, B); and the septa are further peculiar in so far that the wall does not appear to

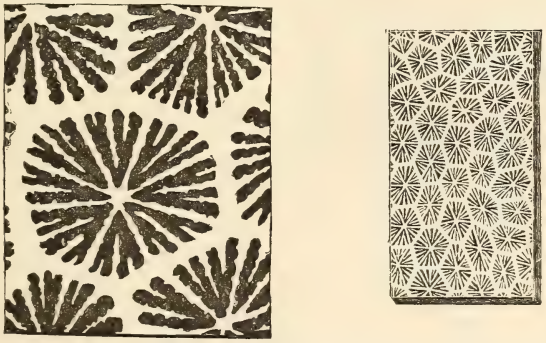


Fig. 149.—*Isastræa oblonga;* portion of a small polished slab, of the natural size, and a few calices enlarged. Jurassic (Portland Oolite).

be formed by an extension and fusion of their outer ends. Lastly, dissepiments in limited number are present, and curved "tabulæ" are well developed (fig. 148, C). The genus is only known as occurring in the Carboniferous rocks of Britain.

The genus *Battersbyia* (with which the *Fascicularia* of Dybowski may be compared) was founded to include certain Devonian corals possessing

a fasciculate corallum, composed of unequally-sized cylindrical corallites, which are not in contact laterally, or only touch each other to a limited extent. According to Professor Martin Duncan, the septa are variable in number and size, and the endothecal tissues consist of an abundance of vesicular dissepiments along with well-developed tabulæ.

In a fourth group of Astræans (*Astrææ cæspitosæ*) the corallum is more or less tufted or cæspitose, the corallites being produced by fission from a common parent, but having their terminal portions free. As examples of this large and well-marked group may be taken the recent *Mussa*, or such Secondary corals as *Thecosmilia* (fig. 146) and *Cladophyllia*, the former of these being one of the most characteristic genera of the Jurassic rocks.

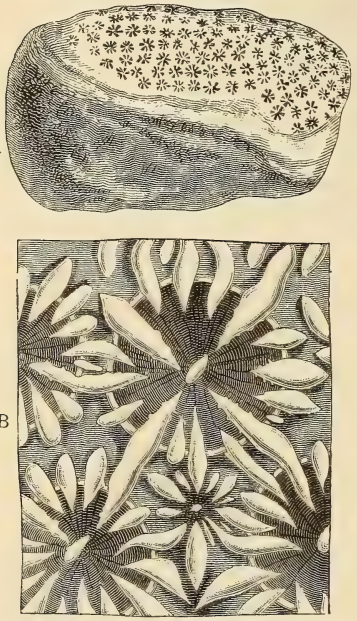


Fig. 150.—A, A small mass of *Holocystis elegans*, of the natural size; B, A few calices of the same, enlarged. Cretaceous. (After Milne-Edwards and Haime.)

In a fifth group (*Astrææ confluentes*) we have a number of well-known genera of Astræans, in which the composite corallum increases mainly by fission, this being so far imperfect that the calices of the different corallites are usually more or less completely confluent with one another. Familiar examples of this group are the genera *Diploria* (Cretaceous to Recent), *Mæandrina* (Jurassic to Recent), *Euphyllia* (Jurassic to Recent), and *Rhipidogyra* (Jurassic and Cretaceous).

All the remaining Astræans are "agglomerate" or "astræiform," consisting of numerous closely approximated corallites, which may be united by their walls directly or by cœnenchyma, and which give rise by their union to massive coralla. In certain of the forms included in this group, such as *Favia* (Jurassic to Recent), the mode of increase is essentially by fission. In others, however, including many of the most typical forms of the entire family, the mode of increase is essentially by gemmation, the new buds being usually thrown out either from the wall or from the calice of the parent. A very large number of generic types of this group are known, abounding in the Secondary and Tertiary periods, and being extensively represented at the present day. Among the more familiar genera may be mentioned *Heliastræa*, *Prionastræa*, *Isastræa* (fig. 149), *Septastræa*, *Convexastræa*, *Plesiastræa*, *Stylina*, and *Latimæandra*.

Finally, we may consider here certain forms of corals which depart more or less widely from the ordinary type of the Astræans, but which are nevertheless to be regarded as belonging to this family. The first of these is the recent genus *Merulina*, in which the corallum is composite and usually foliaceous, with a basal plate which is perforated by foramina and slits. In the possession of this perforated basal plate the genus

approaches the *Fungida*, and it has been commonly regarded as constituting a special family of the *Aporosa* (the *Pseudofungidæ*).

Another remarkable type is constituted by the genus *Holocystis* of the Lower Greensand (Cretaceous). In this genus (fig. 150) the corallum is composite, the corallites being connected directly by their walls or by costæ. There is a styliform columella, and the septa are developed in three cycles, there being four principal septa of much larger size than the others. The symmetry is thus conspicuously tetrameral, and for this reason *Holocystis* has generally been regarded as belonging to the *Rugosa*. The visceral chambers of the corallites are also intersected by tabulæ, these structures being likewise abundantly developed in the allied genus *Coccophyllum* of the Alpine Trias.

The Silurian genus *Stauria*, which has been usually referred to the *Rugosa* (*Tetracoralla*), and which has been regarded as the type of the special family of the *Stauridæ*, may also be regarded as belonging to the *Astræidæ*, since it differs from the typical Astræans in little else than its marked tetrameral symmetry. The corallum in *Stauria* (fig. 151) is

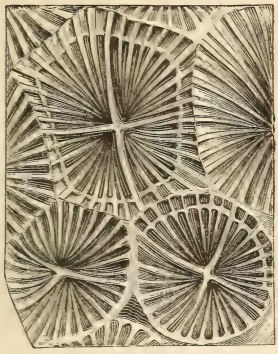


Fig. 151.—A few calices of *Stauria astræiformis*, enlarged, showing the four primary septa forming a four-branched cross. Silurian. (After Milne-Edwards and Haime.)

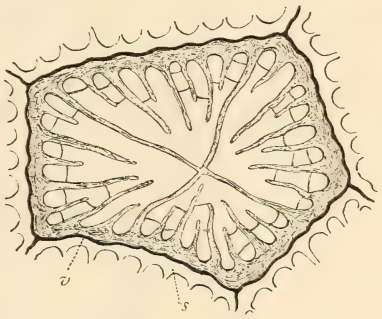


Fig. 152.—Transverse section of a single corallite of *Stauria astræiformis*, from the Silurian of Gotland, enlarged ten times. *v*, Primordial wall; *s*, Secondary layer of stereoplasma, the corresponding layer in the interior of the corallite being shaded. (Original.)

composite and astræiform, increase being effected by calicular gemmation, and the corallites being connected directly by their walls. There is no columella, but there are four principal septa which form a complete cross in each corallite (fig. 152). These four septa divide the visceral chamber into as many quadrants, each of which contains three long and four short septa. The total number of septa is thus thirty-two, sixteen long and sixteen short. The periphery of the visceral chamber is occupied by vesicular dissepimental tissue, while the central area is traversed by horizontal tabulæ. The only known species of this genus is the *Stauria astræiformis* of the Wenlock Limestone.

It would also seem not improbable that the Palæozoic genus *Acervularia*, properly so called (in so far as based upon *Acervularia ananas*, Linn., of the Wenlock Limestone of Gotland), will have to be placed among the *Astræidæ*, though this point does not admit of discussion here. On the other hand, many of the forms usually referred to *Acer-*

vularia are of a different structure to *A. ananas*, and are referable to the Cyathophylloid group of the *Rugosa*.

There does not, further, seem to be any sufficient reason for excluding the Ordovician genus *Columnaria* (=*Favistella*) from the *Astræidæ*. In this genus the corallum (fig. 153) is massive, and is composed of prismatic or polygonal corallites, which are usually more or less completely united by their walls. The septa (fig. 154, A) are well developed, and are lamellar in form, each corallite containing about thirty of these structures, disposed in two cycles, and alternately long and short. The long septa are not of equal length, one being often much longer than the others; and they fall short of the centre of the visceral chamber, no columella being present. Endothecal tissue in the form of dissepiments is very imperfectly developed, but numerous tabulæ (fig. 154, B) are present.

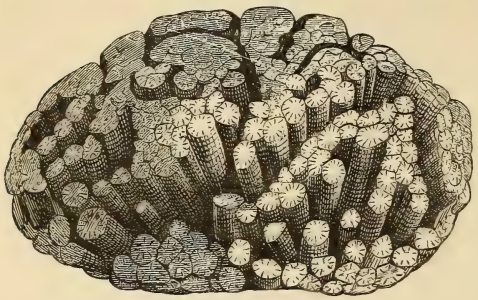


Fig. 153.—A colony of *Columnaria calicina*, Nich., from the Hudson River Group of Canada, of the natural size. (Original.)

Finally, the remarkable recent genus *Moseleya* must be noticed here. In this genus, as described by Mr Quelch, the corallum is

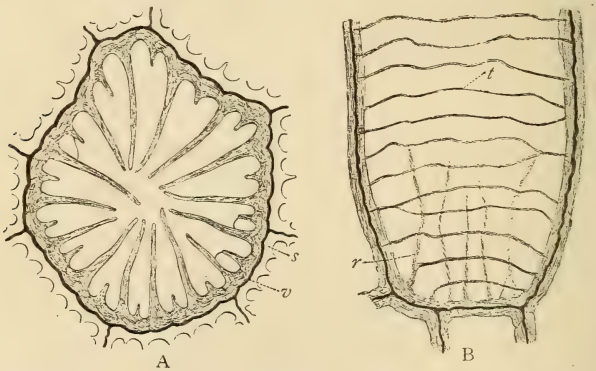


Fig. 154.—Sections of a corallite of *Columnaria calicina*, from the Ordovician of North America, enlarged ten times. A, Cross-section; B, Longitudinal section. *v*, Primordial wall; *s*, Secondary layer of stereoplasma, the corresponding layer in the interior of the corallite being shaded; *t*, Tabulæ; *r*, Cut edges of septa. (Original.)

composite, the only known specimen consisting of a single large corallite, round which smaller corallites are produced by calicinal marginal budding. The wall is very thin, with a slight epitheca; and the septa

are very numerous and are arranged in several cycles, their inner edges being dentate and giving rise superiorly to an irregular pseudo-columella. The septa are not alternately equal, and the symmetry appears to be completely radial. Endothecal tissue is largely developed, the dissepiments being vesicular in the periphery of the visceral chamber, but uniting to form distinct tabulæ centrally. In the possession of an exterior vesicular zone and the presence of a central tabulate area, the genus *Moseleya* resembles the extinct genus *Cyathophyllum ;* and it is referred by Quelch to the family *Cyathophyllidæ*. Upon the strength of this resemblance, indeed, the authority just mentioned refers the *Cyathophyllidæ*, along with the remaining corals usually grouped under the head of *Rugosa*, to the division of the *Madreporaria Aporosa*. It is possible that future researches may justify the merging of the *Rugosa* in the *Aporosa*, but it does not appear in the meanwhile that there is sufficient evidence to warrant a change so sweeping. Even as regards the genus *Cyathophyllum* itself and its immediate allies, the resemblances to *Moseleya* are not without noteworthy counterbalancing differences, as, for example, the general bilateral symmetry of the former, and the usual development of the septa in a pinnate manner along three principal lines. Still more weighty, of course, are the differences which separate the *Zaphrentoidea* and the *Cystiphylloidea* from *Moseleya*. Upon the whole, therefore, as will be more fully shown in what follows, there appears to be sufficient ground for the retention of the *Rugosa* as a special division of the *Madreporaria*, though certain of the Rugose corals of former writers may well be placed among the *Aporosa*.

CHAPTER XVIII.

ZOANTHARIA—continued.

SECTION II. MADREPORARIA RUGOSA (TETRACORALLA).

The corallum in the *Madreporaria Rugosa* may be simple or composite, and is composed of compact, solid sclerenchyma, the theca being complete and imperforate. The septa are usually well developed and lamellar, with smooth or dentated edges; but they are sometimes rudimentary. The symmetry of the corallum is almost always obviously bilateral; and the septa are generally of two orders, alternately long and short. The septa are, typically, developed according to a tetrameral system, new septa being produced along one median and two lateral lines, while a fourth line is commonly marked by a long or short septum or a fossula. A well-marked septal "fossula" is usually present, and generally corresponds with a much reduced primary septum, but there may be three or four fossulæ. Endothecal tissue in the form of dissepiments is usually largely developed; and very generally the dissepiments unite with one another in the central portion of the visceral chamber so as to form well-marked "tabulæ." The mode of increase in the composite coralla is mostly by lateral or calicular budding, and a true cœnenchyma is wanting.

It has been supposed by some naturalists that the so-called Rugose corals might possibly be referable to the *Hydrozoa*, and, at any rate, that they are not truly Madreporarian. On the other hand, Mr Quelch has recently abolished the *Rugosa* as a distinct division, and has united the corals formerly placed therein with the *Madreporaria Aporosa*. Some of the forms included in the old order of the *Rugosa* may, as previously seen, be referred without difficulty to the *Aporosa*, and as regards most of the others the view advocated by Mr Quelch can be supported by evidence of no small weight. The resemblances, namely, between the corallum of the typical *Rugosa* and that of the *Madreporaria Aporosa* are so numer-

ous and so important, that it is impossible to imagine that the coralla in the two cases were secreted by different methods, or bore dissimilar relations to the soft parts of the animals producing them. Thus, in both groups alike the simple form of corallum (fig. 155) consists of an outer wall or "theca," enclosing a central space or "visceral chamber," which is ordinarily divided into a series of compartments by vertical partitions or "septa"; in both alike the "visceral chamber" may be partitioned off into storeys by horizontal plates or "tabulæ"; in both alike the interseptal loculi are liable to be more or less subdivided by "dissepiments"; and in both alike

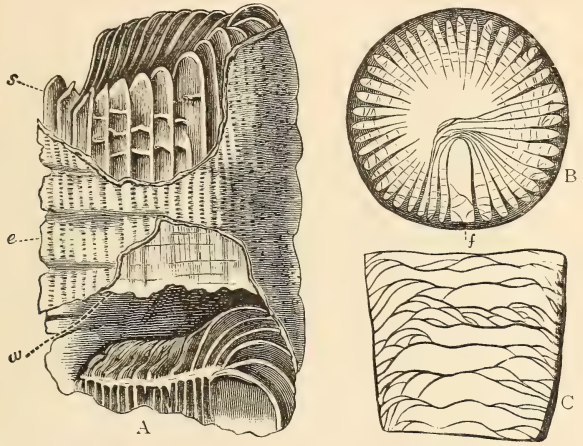


Fig. 155.—Morphology of the *Rugosa*. A, Fragment of *Zaphrentis gigantea*, showing the septa (*s*), with the sparse dissepiments crossing the interseptal loculi, the epitheca (*e*), and the thin proper wall (*w*); B, Transverse section of *Zaphrentis Guerangeri*, showing the septa and dissepiments, the central area occupied solely by the tabulæ, and the "fossula" (*f*); C, Longitudinal section of the last, showing the arrangement of the tabulæ. (A is after Edwards and Haime; B and C are after Mr James Thomson.)

the axial rod, known as the "columella," may be developed. In both groups, moreover, the corallum is often composite, and may be regarded as a variously formed aggregate of "corallites," each of these subordinate elements of the colony being essentially similar in structure to the typical simple corallum.

In spite of the above-mentioned general resemblances, it will be found, however, that the central and most typical group of the old order *Rugosa*—viz., the group of the Zaphrentoid corals—is separated from the division of the *Madreporaria Aporosa* by important morphological and developmental characters. But the Zaphrentoids are very intimately connected by many intermediate links with the *Cyathophylloidea*, the group of *Rugosa* which most nearly approaches the *Astræidæ*. The Cyathophylloids, again, have a

close connection with the typical *Cystiphylloidea*, and, through these, with the most abnormal of all the forms included in the *Rugosa* (viz., *Calceola* and its allies). Upon the whole, therefore, in the present condition of our knowledge, it seems best to retain the name *Rugosa* for the three groups of the Zaphrentoid, Cyathophylloid, and Cystiphylloid corals, and to regard these as constituting a special division of the *Madreporaria*.

While the corallum of the *Rugosa*, as above limited, is in general structure quite similar to that of the *Madreporaria Aporosa*, it possesses certain special peculiarities, which must be briefly noticed here. The structure of the *theca* or wall of the corallum in the *Rugosa* is generally in agreement with that of the *Aporosa*, the outer investment of the visceral chamber being formed by the coalescence of lateral outgrowths from the peripheral margins of the septa, as seen, for example, in *Zaphrentis* (fig. 127, C). In other cases (as in *Heliophyllum* and *Crepidophyllum*), the septa appear to end abruptly in the wall, which is very thin, and seems to be developed independently of the septa. In *Streptelasma*, again, a dense false wall is formed by the junction of the much-thickened outer ends of the septa (fig. 127, B). A true "epitheca" has been very commonly described as present in the simple Rugose Corals, but it is very difficult to demonstrate the existence of this in microscopic sections, as a structure distinct from the true wall, and it seems probable that what has been generally called the "epitheca" is in many cases really the "theca." In certain of the compound Rugose Corals, on the other hand, there exists a general epitheca enclosing the entire colony inferiorly. As regards their internal structure, the septa are usually composed, as in the *Aporosa* generally, of a median plate ("primordial septum") bounded on both sides by a layer of dense secondary sclerenchyma or "stereoplasma." In some cases, as in *Pholidophyllum*, the septa can be shown to be formed by the coalescence of obliquely directed calcareous trabeculæ, the free ends of which project at the inner margins of the septa. In *Heliophyllum* and its allies, the septa are thin, and are either unthickened by secondary stereoplasma, or have only a very thin layer of this substance on the sides of the primordial septum. In these cases the oblique trabeculæ ("Septaldornen" of the Germans) above spoken of are greatly developed, and give rise to the peculiar structures known as "carinæ," which will be more fully considered later on.

The most important features in the structure of the corallum of the *Rugosa* are, however, connected with the arrangement and mode of development of the septa. The most obvious of the peculiarities of a typical Rugose coral is the conspicuously bilateral disposition of its parts (see fig. 139). The causes of this bilaterality will be best understood by a consideration of the structure of a simple Rugose

coral, such as *Streptelasma corniculum* or *Omphyma subturbinata*. From an investigation of such types it was shown by Kunth that the symmetry of the corallum is tetrameral, and is governed by four principal septa placed at right angles to one another. The bilaterality of the corallum depends upon the mode in which new septa are developed in relation to three out of these four principal septa. The most important of the three principal septa in question is placed along the convex (or "dorsal") side of the corallum, and new septa are developed on both sides of this in a pinnate or feather-like manner (fig. 156, A). This dorsal median septum may be longer or shorter than the other septa, or of normal size, and it may be con-

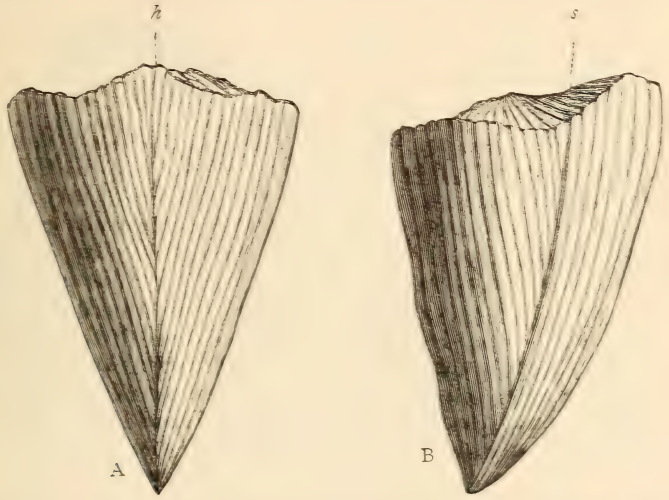


Fig. 156.—A, *Streptelasma corniculum*, viewed from its convex (or "dorsal") side, showing the intercalation of new septa on both sides of the "cardinal septum" (*h*), of the natural size. B, Side-view of the same specimen, showing the development of new septa on one side of one of the "alar" septa (*s*). From the Ordovician rocks of North America. (Original.)

veniently spoken of as the "cardinal septum" (the "Hauptseptum" of Kunth). The septa produced on the two sides of the "cardinal septum" gradually get less and less oblique to the latter, till we reach two septa placed laterally, at right angles to the "cardinal septum," which may be spoken of as the "alar" septa (the "Seitensepta" of Kunth). On the ventral side of each alar septum—*i.e.*, on the side furthest removed from the "cardinal septum"—new septa are developed in an oblique manner (fig. 156, B, *s*). The remaining septum of the quartette of principal septa is placed in the middle line on the concave (or "ventral") side of the corallum, and it does not serve as a starting-point for the development of new septa, and therefore

does not show any feather-like disposition of the septa on its sides. It may be longer or shorter than the others, and may be spoken of as the "counter" septum (the "Gegenseptum" of Kunth).

Hence, the surface of the theca of a simple Rugose coral such as *Streptelasma corniculum* is marked out by these four principal septa into as many quadrants, as shown in the annexed sketch (fig. 157) of a specimen of this coral, viewed from the base, and therefore greatly foreshortened. Thus the dorsal or convex side is divided into two "cardinal" quadrants, occupied by the pinnately developed septa which flank the "cardinal septum" (fig. 157, *h*). The two

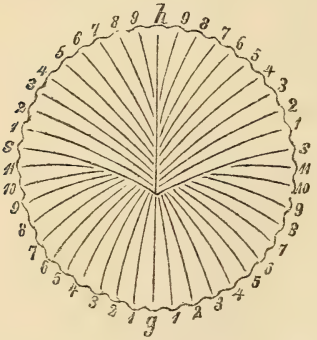


Fig. 157.—Plan of the septa in a specimen of *Streptelasma corniculum*, viewed from below, the radiating lines indicating the peripheral margins of the septa as appearing on the surface of the corallum. *h*, The "cardinal septum"; *ss*, The "alar" septa; *g*, The "counter septum." (After Kunth.)

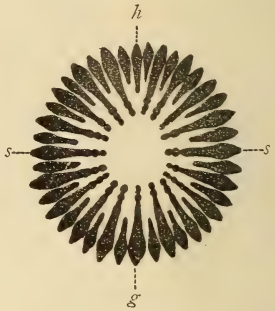


Fig. 158.—Transverse section of *Palæocyclus porpita*, from the Silurian of Gotland, enlarged three times. *h*, "Cardinal" septum, contained in the fossula; *ss*, "Alar" septa; *g*, "Counter" septum. In the section figured there are only forty septa, but there are usually forty-four, twenty-two long and twenty-two short. (Original.)

"counter" quadrants, on the other hand, are occupied by the septa developed along the ventral side of the "alar" septa (fig. 157, *ss*), and they merge with one another in the mesial ventral line, owing to the fact that the "counter septum" (*g*) is not a source for the development of new septa. It follows from the above that an inspection of the surface of a well-preserved example of *Streptelasma corniculum* or *Omphyma subturbinata* enables us to recognise by the disposition of the septa the position of the "cardinal" and "alar" septa, but that the "counter septum" cannot be thus recognised.

It was further pointed out by Kunth that though the four principal septa above spoken of divide the corallum into four quadrants, it does not necessarily follow that these contain the same number of septa each. On the contrary, it is not unusual to find that the "counter quadrants" contain conjointly a greater number of septa than do the two "cardinal quadrants."

Thus in *Palæocyclus porpita* (fig. 158), the number of septa in each quadrant is sometimes the same—namely, nine—making, with the four principal septa, a total of forty. In most examples of this coral there are, however, forty-four septa in all, the two counter-quadrants containing each eleven septa, while the cardinal quadrants have nine each.

The peculiar arrangement of the septa above indicated can be recognised in a large number of the simple Rugose corals by a mere inspection of the surface of well-preserved examples. Where the surface is badly preserved, and the observer has to rely upon thin sections, the "cardinal" and "counter" septa can usually be readily recognised, but it is often a matter of difficulty to determine the "alar" septa. In some of the most completely radial forms—as in some species of *Cyathophyllum*—the position of the four principal septa may cease to be recognisable in transverse sections of the corallum. Lastly, in cases where the septa are rudimentary—as in the Cystiphylloids generally—it may be impossible to demonstrate the tetrameral arrangement of the septa, though in other cases (as in *Goniophyllum*) no such difficulty obtains.

As regards the relative *length* of the septa, the most usual arrangement is to find that the septa are alternately equal (approximately equal, that is to say); so that the septa consist of a long series and a short series alternating with one another. Hence, the septa are often said to be of two "orders," but the septa of each order are by no means always quite equal in length, nor is it to be supposed that the septa of each order were simultaneously developed.

In a great many of the *Rugosa*, the bilaterality of the corallum is especially marked by the unequal development, as regards length, of the "cardinal" and "counter" septum, one or other of which usually occupies the so-called "fossula." The "fossula" or "fossette" (fig. 139), as previously explained (see p. 262), is a more or less conspicuous groove or depression in the calice, due to a reduction in size of the septa at that point, necessitated, in all probability, by the existence in the living polype of one or more hypertrophied mesenteries carrying the reproductive organs. As a rule, there is only one "fossula," which may be median or lateral in position, the latter being, however, very unusual. Sometimes there are three fossulæ, one median, and two lateral; while in other cases (*e.g.*, *Omphyma*) there are four of these calicine grooves, two median, and two lateral. In this last case (fig. 159, A), the four fundamental septa occupy the four fossulæ, the cardinal septum being the best developed. In the much more common case of there being only a single median fossula, this is almost always related to either the "cardinal" or the "counter" septum. The most usual arrangement is for the fossula to be placed on the convex (or "dorsal") side of the simple coralla, in which case it is intersected mesially by the "cardinal septum," which is then much *reduced in size*. This disposition of parts occurs in *Palæocyclus porpita* (fig. 158), in the genus *Streptelasma*, and in most of the species usually referred to *Zaphrentis*. Sometimes, as in *Lophophyllum*, the "cardinal" septum is very short, and occupies the dorsally-placed fossula,

while the "counter" septum is especially long. On the other hand, the fossula may be placed on the concave (or "ventral") side of the simple coralla, as in some of the species generally placed in *Zaphrentis* (*e.g.*, in *Zaphrentis Enniskilleni*, fig. 139). In this case the fossula is intersected by the "counter" septum, which is reduced in size, or may be altogether rudimentary or obsolete; while the "cardinal" septum may have its normal dimensions, or may be specially developed. In rare cases the fossula (when single) is lateral in position, and is occupied by one of the "alar" septa.

The interseptal loculi in the Rugose corals are generally more or less largely occupied by endothecal tissue in the form of dissepiments and tabulæ, both these structures being usually conjoined. The dissepiments are principally developed in the peripheral area

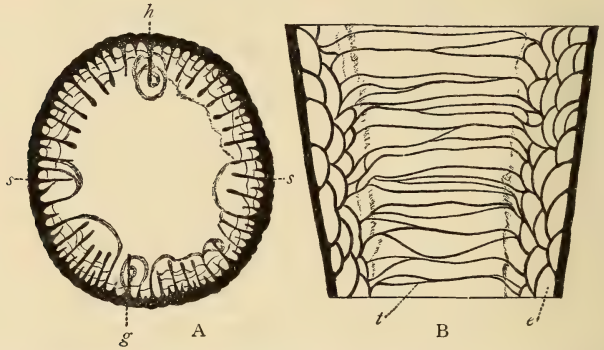


Fig. 159.—Structure of *Omphyma subturbinata*, from the Silurian of Britain. A, Transverse section, enlarged slightly, showing the four fossulæ, the arrangement of the septa, and the large central area occupied by the tabulæ: *h*, Cardinal septum; *ss*, Alar septa; *g*, Counter septum. B, Longitudinal section, slightly enlarged: *e*, Peripheral zone of vesicular dissepimental tissue; *t*, Tabulæ. (Original.)

of the visceral chamber, and have the form of curved calcareous plates directed obliquely from one septum to the next one. In transverse sections (fig. 159, A) the cut edges of the dissepiments appear as transverse lines passing directly or in a curved manner across the interseptal loculi, and connecting together adjacent septa. In longitudinal sections (fig. 159, B) the dissepiments are usually seen to give rise to an outer zone of lenticular vesicles (*e*) which are directed obliquely inwards and downwards from the internal surface of the wall towards the centre of the visceral chamber. In the central region of the corallum the dissepiments become more nearly horizontal and are developed in adjacent interseptal loculi at the same level, their coalescence giving rise to the flat or curved transverse partitions which are known as "tabulæ" (fig. 159, B, *t*). The central tabulate area of the visceral chamber varies much in extent, but is best developed in those types (such as *Amplexus*,

Omphyma, *Campophyllum*, &c.) in which the septa are short and do not extend far from the wall inwards.

The development of the peripheral zone of vesicular dissepimental tissue is also very variable, its extent being in inverse proportion to that of the central tabulate area. It is very well developed in *Cyathophyllum* and in the *Cyathophylloid* corals generally, though considerably reduced in such types as *Omphyma* and *Campophyllum*. In *Zaphrentis* and the Zaphrentoid corals in general the dissepimental vesicular zone is greatly reduced, and may be practically absent, the central tabulate area being greatly developed. On the other hand, in *Cystiphyllum* and its immediate allies the central tabulate area is invaded by the dissepiments, and the entire visceral chamber becomes filled with a vesicular tissue, the central cells of which are usually of comparatively large size, and represent tabulæ. In *Palæocyclus porpita*, and in some very flat discoid types (such as *Microcyclus*), the depth of the visceral chamber is insufficient to permit of the development of dissepiments or tabulæ. These structures are likewise obsolete in the aberrant genus *Calceola;* while they are very imperfectly developed in the genus *Lindstrœmia*, owing to the fact that the lower part of the visceral chamber becomes filled by secondary stereoplasma.

As regards exothecal structures, the corallum of the Rugose corals generally exhibits externally more or less conspicuous vertical ridges, which are spoken of as "rugæ," and which are separated by intervening depressions or grooves. In some cases, these longitudinal ridges may correspond with the outer edges of the septa within, and may thus resemble the structures known in the Aporose corals as "costæ." In most cases, however, the ridges correspond with the interseptal loculi, and thus alternate with the septa. In some cases (*e.g.*, in *Pholidophyllum*) Lindström has described the vertical ridges as carrying rows of minute, overlapping, calcareous plates or scales. Other superficial exothecal structures are occasionally developed in Rugose corals, such as the surface-tubercles of some species of *Zaphrentis*, the root-like processes of attachment of *Omphyma*, &c., and the connecting-processes which unite adjacent corallites in *Eridophyllum*. The remarkable opercular plates of such genera as *Goniophyllum* and *Calceola* must also be regarded as of an exothecal nature. It must be regarded as doubtful, however, if anything which can properly be described as a "cœnenchyma" is developed in any composite Rugose coral. In such types, the corallites may remain isolated except at their point of origin from the colony; or, if in contact, they may either be united by the fusion of their walls, or the walls may be absent and the corallites are united to one another by the extension and confluence of their septa, as seen, for example, in the genus *Phillipsastræa* (fig. 160).

As regards their *classification*, the *Rugosa* are here considered as a mere section of the *Madreporaria*, instead of as a distinct order of Corals, and the signification of the name has been considerably

narrowed by the removal to the *Aporosa* of various types originally referred to this group. Thus, the Palæozoic genera *Stauria* and *Cyathaxonia*, previously generally placed among the *Rugosa*, are here relegated to the *Aporosa*, while Professor Martin Duncan has been followed in the reference to the same group of the Secondary genus *Holocystis*, the Tertiary *Conosmilia*, and the recent *Haplophyllia* and *Guynia*. As thus limited, the *Rugosa* constitute a moderately natural assemblage of forms, which may be subdivided into three main

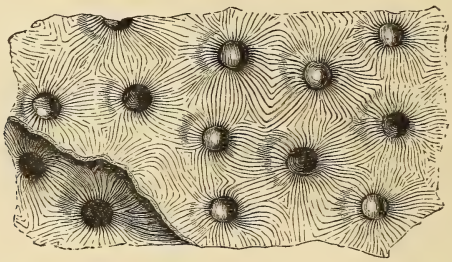


Fig. 160.—*Phillipsastræa Verneuilli*. From the Devonian (Corniferous Limestone) of N. America. (After Billings.)

sections, which are typified respectively by the genera *Cyathophyllum*, *Zaphrentis*, and *Cystiphyllum*, and which may therefore be spoken of as the *Cyathophylloidea*, *Zaphrentoidea*, and *Cystiphylloidea*.[1] As regards their *distribution in time*, all these groups are confined, so far as at present certainly known, to the Palæozoic period, and their characters and principal types will now be briefly considered.

I. Cyathophylloidea.

The section of the *Cyathophylloidea* comprises those *Rugosa* in which the peripheral region of the visceral chamber is more or less extensively occupied by vesicular dissepimental tissue, the lenticular cells of which are directed obliquely inwards and downwards, their convex sides being turned upwards (fig. 161, B). The central area of the visceral chamber is occupied by tabulæ, but the tabulate area is often much restricted. The length of the septa is very variable, but these structures are always present and are generally alternately long and short, the septa of each order being approximately equal. In most forms there is a well-developed fossula, and the symmetry is conspicuously bilateral. In others the fossula is rudimentary or

[1] The elaborate classification of the Rugose corals put forward by Dybowski has not been adopted here, partly because many of the forms placed in this group by this observer are here removed elsewhere, and partly because the details of his proposed arrangement are largely unnatural.

obsolete, and the symmetry becomes more or less radial. A true columella may or may not be present, and the corallum may be simple or composite.

The Cyathophylloids, so far as certainly known, are confined to the Ordovician, Silurian, Devonian, and Carboniferous deposits, and are thus wholly Palæozoic.

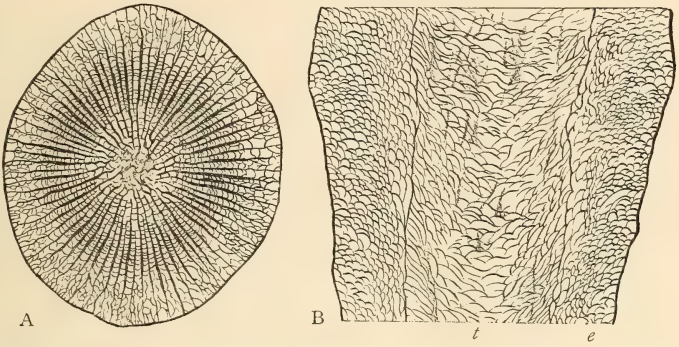


Fig. 161.—Structure of *Cyathophyllum heterophyllum*, from the Middle Devonian of Gerolstein. A, Transverse section of the corallum, slightly enlarged; B, Longitudinal section, also slightly enlarged, showing the outer vesicular zone (*e*), and the central area of anastomosing tabulæ (*t*). This is one of the species of *Cyathophyllum* in which a "fossula" is not clearly recognisable, the symmetry thus becoming completely radial. The septa nearly reach the centre, and their inner portions are considerably thickened. (Original.)

Upon the ground of a close structural resemblance between the genus *Cyathophyllum* itself and the recent genus *Moseleya*, Mr Quelch, as previously noted, has proposed the removal of all the *Cyathophyllidæ* to the Aporose Madreporarians, and the placing them in the immediate vicinity of the *Astræidæ;* but this change can hardly be accepted. It is true that there are certain species of *Cyathophyllum* which are so far similar to *Moseleya* that they show an almost complete radial symmetry, a "fossula" not being distinctly developed, while a tetrameral arrangement of the septa is not recognisable. Even within the limits of the genus *Cyathophyllum* itself, there are, however, species with a well-developed fossula and a distinctly bilateral arrangement of parts; while other allied genera are as conspicuously bilateral as is the genus *Zaphrentis*, and possess a "fossula" of precisely the same type as that of the latter. Moreover, through such genera as *Omphyma* and *Campophyllum* a complete transition is effected between the typical Cyathophylloids and the typical Zaphrentoids. Lastly, through *Cystiphyllum* it becomes easy to pass from *Cyathophyllum* or *Actinocystis* to such aberrant types as *Goniophyllum* and *Rhizophyllum*.

Family 1. *Cyathophyllidæ*.—The chief family of the Cyathophylloid corals is that of the *Cyathophyllidæ*, comprising all those members of the present section in which the septa are smooth, and consist of a median plate ("primordial septum") thickened on both sides by a layer of stereoplasma or secondary calcareous deposit.

Of the many genera of this family the three leading types are *Cyathophyllum*, *Lithostrotion*, and *Omphyma*.

In the genus *Cyathophyllum* itself, the corallum may be simple or composite, the compound forms being sometimes massive (fig. 162), sometimes fasciculate. The septa are numerous, alternately long and short, the longer ones being continued to, or nearly to, the centre of the visceral chamber, where they are usually more or less twisted, and give rise to a sort of spurious columella (fig. 161, A). The external dissepimental zone is largely developed, and is composed of oblique vesicles of small size (fig. 161, B); while the internal tabulate area is comparatively small and incompletely developed, the tabulæ having a vesicular character. The "fossula" is small or obsolete, the symmetry in the latter case becoming more or less completely radial; whereas when the fossula is recognisable, the symmetry is obviously bilateral. Many species of the genus are known, the earliest forms appearing in the Ordovician and the latest in the Carboniferous rocks. The genus is especially well represented in the Devonian and Carboniferous rocks.

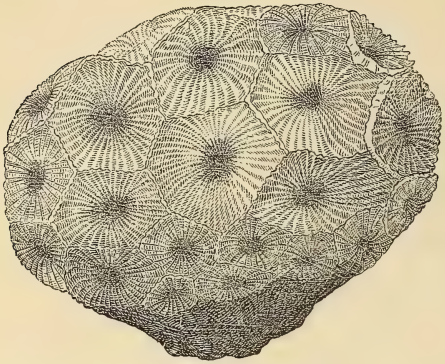


Fig. 162.—A specimen of *Cyathophyllum hexagonum*, from the Devonian Limestone of Gerolstein, of the natural size. (After Zittel.)

The Silurian and Devonian genus *Actinocystis* differs from *Cyathophyllum* proper, chiefly in the fact that the septa are imperfect, passing

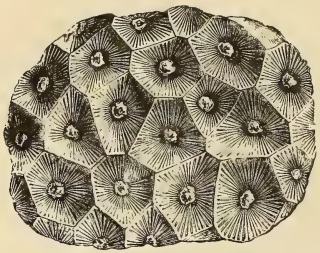


Fig 163.—*Arachnophyllum* (*Strombodes*) *pentagonum*. Silurian, Canada.

Fig. 164.—*Arachnophyllum* (*Strombodes*) *gracile*. Silurian, Canada.

externally into vesicular tissue, which also largely replaces the central tabulate area. Allied genera are the *Spongophyllum* and *Endophyllum* of the Devonian rocks, in which the corallum is composite, and the septa are also more or less incomplete.

The genus *Acervularia*, as based on the *A. ananas* of the Silurian

rocks, may perhaps be referred, as previously remarked, to the *Astræidæ;* but many of the astræiform corals usually placed in this genus, and especially the so-called "*Acervulariæ*" of the Devonian rocks, are nearly allied to *Cyathophyllum*. The corals in question agree in general structure, and particularly in the possession of an exterior vesicular zone, with *Cyathophyllum*, but differ from this in the fact that the central tabulate area is partitioned off and enclosed by a secondary and interior wall or "mural investment." Another type which may be placed in this neighbourhood is the Silurian genus *Arachnophyllum* (= *Strombodes*), in which the corallum is composite and astræiform (figs. 163 and 164), but the walls of the corallites, as also the septa, are very imperfectly developed, while the visceral chamber is almost filled with vesicular tissue disposed centrally in funnel-shaped layers.

As the type of another group of the *Cyathophyllidæ*, the great genus *Lithostrotion*, so characteristic of the Carboniferous deposits of many parts of the world, may be taken. The corallum in this genus (fig. 165) is always composite, sometimes massive, sometimes fasciculate, according as the prismatic or cylindrical corallites are or are not in direct contact with one another. In internal structure, *Lithostrotion* is built upon the type of *Cyathophyllum*, each corallite having an external vesicular zone and an internal tabulate area (fig. 166, B). The vesicular zone is narrow, and the tabulate area is wide, and is traversed centrally by a well-developed styliform columella. The septa are alternately long and short, their disposition being clearly tetrameral; and the symmetry is distinctly bilateral, a well-marked fossula being often recognisable. Thus, in the species here figured (fig. 166, A), there are fifty-six septa in all in each corallite, twenty-eight of these being long ones and a similar number being short. Of the twenty-eight long septa, the four leading septa are readily determined. The "cardinal septum" (*h*) is shorter than the others, and is placed in the fossula, while the "counter septum" (*g*) is placed at the opposite end of the compressed columella, a definite middle line to the corallite being thus established. At right angles to the centre of this line are the two "alar septa" (*s s*), and the remaining twenty-four long septa form four groups of six septa each, corresponding with the four quadrants of the corallite. Some of the species of *Lithostrotion* are not as regularly constructed as the above, but the same general type is preserved throughout the genus.

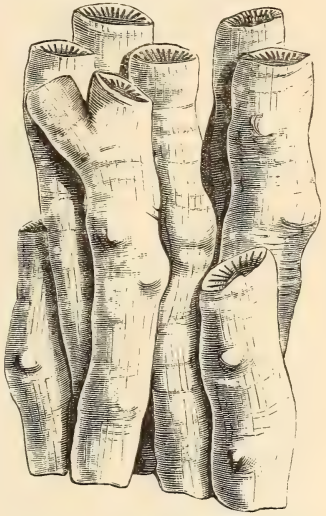


Fig. 165.—Fragment of a mass of *Lithostrotion Martini*, of the natural size. Carboniferous. (After De Koninck.)

The genus *Diphyphyllum*, ranging from the Silurian to the Carboniferous, appears to resemble *Lithostrotion* in general structure, but the corallites of the fasciculate corallum are devoid of a columella. The genus *Eridophyllum*, of the Silurian and Devonian rocks, again, seems to differ from *Diphyphyllum* principally in the fact that the long, cylin-

drical corallites are united together by horizontal connecting-processes of an exothecal nature.

Lastly, a natural transition is effected between the typical Cyathophyllids and the typical *Zaphrentidæ* by means of such genera as

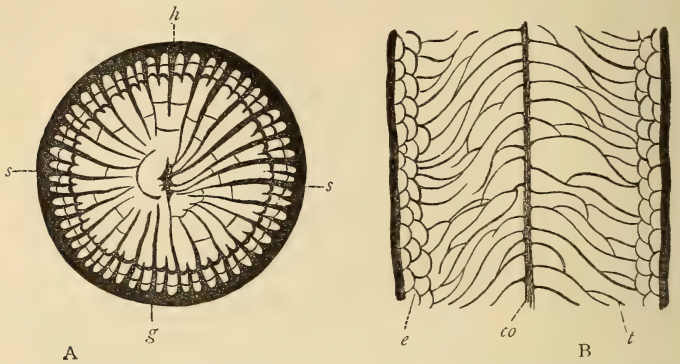


Fig. 166.—Structure of *Lithostrotion Martini*, from the Carboniferous Limestone. A, Transverse section, enlarged about 3½ times; B, Vertical section, similarly enlarged. *h*, Cardinal septum, situated in the fossula; *g*, Counter septum; *ss*, Alar septa: *co*, Columella; *e*, Vesicular tissue; *t*, Tabulæ. (Original.)

Omphyma and *Campophyllum*. The genus *Omphyma* is wholly confined to the Silurian rocks, and comprises simple, turbinate or cylindro-conical corals, the wall of which gives out root-like processes of attachment of an exothecal nature (fig. 167, *a*). The calice shows four shallow fossulæ, placed at right angles to one another, and lodging the four leading septa; and the same structure is shown in transverse sections of the corallum (fig. 159, A). The septa are numerous, and are alternately long and short; but even the longest septa extend a limited distance only into the visceral chamber, thus leaving a very extensive central area, which is occupied by the tabulæ (fig. 159, B). The genus agrees in this respect with the Zaphrentoids, but it shows its relationship with *Cyathophyllum* by the possession of an external zone of vesicular tissue, though this is comparatively of small thickness, and is

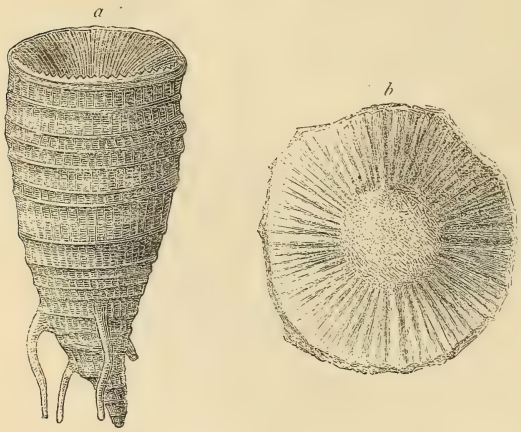


Fig. 167.—*Omphyma subturbinata*, from the Silurian of Gotland, reduced in size. *a*, Side view of the corallum: *b*, View of the calice showing the four fossulæ. (After Milne-Edwards and Haime.)

composed of comparatively large vesicles. In the reduction of the external vesicular zone and the proportionate development of the central tabulate area, the Devonian and Carboniferous genus *Campophyllum* closely resembles *Omphyma*, and also approaches the Zaphrentoids. The genus further resembles these latter, and differs from *Omphyma*, in the possession of a single very large fossula, giving rise to a conspicuous bilaterality of the corallum.

Family 2. *Heliophyllidæ*.—The members of this family agree in many respects with the typical *Cyathophyllidæ*, but are markedly distinguished from these by the characters of the septa. These structures in the present family are thin, and are composed essentially of nothing more than the primordial septal plate, occasionally with a thin coating of stereoplasma towards their bases. The septa are thickened on their sides by conspicuous lamellar ridges (representing the septal spines of such forms as *Pholidophyllum*), which are directed obliquely inwards and upwards from the exterior of the visceral chamber towards the centre of the same, and which

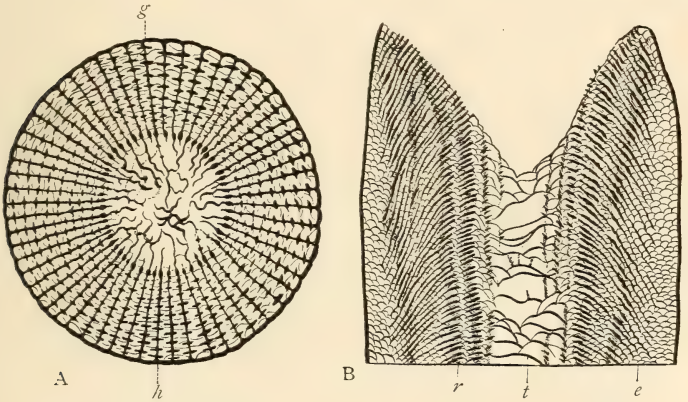


Fig. 168.—Structure of the corallum of *Heliophyllum elegantulum*, from the Devonian (Hamilton Group) of North America. A, Transverse section, enlarged nearly twice; B, Longitudinal section of the same, taken just below the calice, similarly enlarged. *h*, Cardinal septum, in the fossula; *g*, Counter septum; *e*, Peripheral vesicular zone; *t*, Central tabulate area; *r*, Oblique septal ridges ("carinal ridges") on the sides of the septa. (Original.)

form a marked feature in longitudinal sections of the corallum (fig. 168, B). In transverse sections of the corallum (fig. 168, A) these oblique septal ridges appear as conspicuous cross-bars or "carinæ,"[1] which run transversely to the septal laminæ and produce a most characteristic appearance. On the free edges of the septa, again, the septal ridges appear as prominent transverse ridges or teeth. Owing to the development of the septal ridges just spoken of, the septal

[1] The appropriate name of "carinæ" was given to these septal bars by Miss Mary E. Holmes, M.A.

laminæ often become more or less zigzag in the peripheral part of the corallum.

As regards the other characters of the *Heliophyllidæ*, the outer ends of the septa terminate with apparent abruptness in a thin outer investment, which is not improbably rather of the nature of an epitheca rather than of a true "wall.' In some cases (*Phillipsastræa*) the corallites have no definite outer investment, the septa of adjacent tubes becoming confluent. As in the *Cyathophyllidæ*, there is a well-developed external vesicular zone, and a comparatively small central tabulate area. The range of the family is from the Silurian to the Carboniferous, but the great majority of the species are Devonian, the group being, as a whole, as characteristic of the Devonian period as the family of the *Clisiophyllidæ* is of the succeeding Carboniferous period. The three leading genera are *Heliophyllum*, *Crepidophyllum*, and *Phillipsastræa*.

In the genus *Heliophyllum* itself the corallum is simple (fig. 169) or composite; the carinate septa are numerous and alternately long and short, the latter, however, being of considerable length; and the longer septa are, many of them, continued inwards to near the centre of the visceral chamber, where they become twisted, and coalesce to form a spurious columella, which is of large size, and often projects prominently into the floor of the calice (fig. 168, A). The symmetry of the corallum is distinctly bilateral, a well-marked "fossula" being present. The "cardinal septum" is shorter than the other long septa, and, along with two short septa, occupies the fossula. The exterior vesicular zone is well developed, dissepiments being exceedingly abundant, and there is a small tabulate central area (fig. 168, B). The species of the genus are principally Devonian, but some Silurian corals have also been referred here. The genus *Heliophyllum* has commonly been regarded as a mere subgenus of *Cyathophyllum*, but if due weight be given to the peculiar structure of the septa, it can hardly be placed in the family of the *Cyathophyllidæ* at all. The genus *Crepidophyllum* is in general structure essentially similar to *Heliophyllum*, but the central tabulate area is enclosed in a distinct accessory wall or inner mural investment, which is usually open on one side so as to communicate freely with the large fossula (fig. 128, B). The corallum may be simple or compound, and all the known species of the genus are found in the Devonian rocks.

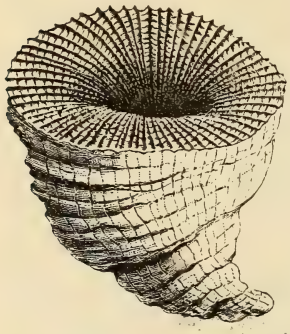


Fig. 169.—A young form of *Heliophyllum Halli*, viewed from one side. Devonian. Of the natural size. (Original.)

Lastly, in the genus *Phillipsastræa* (=*Smithia*) the corallum is compound, and the internal structure of the corallites is essentially the same as in *Heliophyllum*.[1] The corallites, however, are devoid of a wall, and

[1] This statement is based on a microscopic examination of *Phillipsastræa Verneuilli*, of the American Devonian rocks, the type-species of the genus.

become united to one another by the confluence of the outer ends of the septa (fig. 160). The septa are "carinate," and alternately long and short, a distinct fossula being usually present, and the symmetry thus becoming clearly bilateral. The species of *Phillipsastræa* are principally Devonian, but the range of the genus extends into the Carboniferous period.

Family 3. *Clisiophyllidæ*.—The corals of this family agree with the *Cyathophyllidæ* and *Heliophyllidæ* in the general character of possessing a well-marked exterior vesicular zone and a central tabulate area. The central tabulate area is, however, traversed in this family by an extensively developed and complex spurious columella, formed partly of vertical, often twisted plates which have a general radial direction, and partly of vesicular tabulæ which intersect the former in an obliquely ascending direction. This massive pseudo-columella appears in the floor of the calice as a rounded or conical boss of greater or less size, the surface of which, in well-preserved specimens, shows radiating, often spiral ridges. The septa are numerous, of two sizes, alternately equal. The symmetry is usually markedly bilateral, a well-developed "fossula," lodging the "cardinal

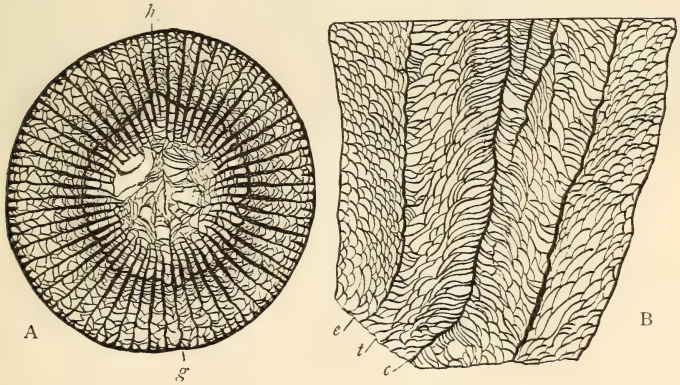


Fig. 170.—Morphology of the *Clisiophyllidæ*. A, Transverse section of *Dibunophyllum* sp., from the Carboniferous rocks of the North of England, slightly enlarged; B, Longitudinal section of the same. *h*, "Cardinal septum" situated in the "fossula"; *g*, "Counter septum"; *e*, Outer zone of vesicular dissepiments; *t*, Central area of anastomosing tabulæ; *c*, The columellar plate. (Original.)

septum," being present. The "cardinal septum" is shorter than the other long septa, and the "counter septum" is often specially developed. The septa are thickened by lateral deposits of stereoplasma, and are not "carinate." The corallum may be simple or composite. The *Clisiophyllidæ* are mainly, if not exclusively, confined to the

Milne-Edwards and Haime state that a columella is present, but no traces of this structure appear in thin sections.

Carboniferous period, the principal genera being *Clisiophyllum*, *Dibunophyllum*, *Cyclophyllum*, *Aulophyllum*, and *Lonsdaleia*.

In the genus *Clisiophyllum* the general structure of the simple corallum is as described in the above characterisation of the family *Clisiophyllidæ*. The great central pseudocolumellar mass is composed of a number of tolerably regular, radial and somewhat spiral lamellæ, which may be regarded as corresponding with prolongations of the septa, and which are intersected by obliquely directed vesicular tabulæ (fig. 171, B). As seen in the floor of the calice, the pseudocolumella forms a large rounded boss, marked by spiral radiating ridges. The zone immediately external to the pseudocolumella is occupied by inosculating tabulæ,

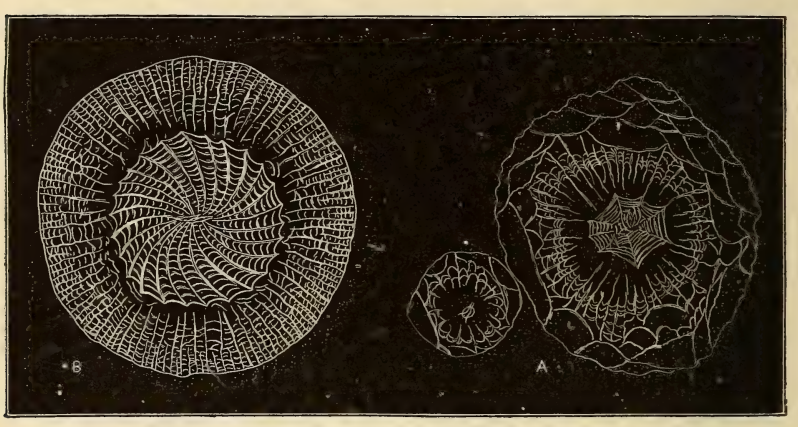


Fig. 171.—A, Cross-section of two corallites of *Lonsdaleia duplicata*, Lower Carboniferous, enlarged; B, Cross-section of the corallum of *Clisiophyllum Keyserlingi*, Lower Carboniferous, of the natural size. (After James Thomson and the Author.)

forming large vesicles; and external to this region is a deep peripheral zone of small oblique dissepimental vesicles, traversed by the septa. The septa are numerous, alternately long and short, and a well-marked septal fossula is present. The species of *Clisiophyllum* are probably wholly confined to the Carboniferous period, though some Devonian and Silurian corals have been referred here.

The Carboniferous genus *Dibunophyllum* (fig. 170) is very closely related in general structure to *Clisiophyllum*, but the pseudocolumellar area is divided into two by a vertical partition, or columellar plate, one end of which is usually connected with the "counter septum," while the other is directed to the "cardinal septum" in the fossula, the bilateral symmetry of the corallum being thus exceedingly well marked. Again, in the Carboniferous genus *Aulophyllum*, and the nearly allied or identical *Cyclophyllum*, the pseudocolumellar area is enclosed by a kind of inner mural investment or accessory wall, and is prolonged at one point into a lateral tongue-like extension directed to the fossula. The pseudocolumella has a minutely vesicular structure, the vesicles being formed by radial lamellæ intersected by obliquely ascending arched dissepiments. *Aulophyllum* stands in the same relation to *Clisiophyllum* that *Crepidophyllum* holds to *Heliophyllum*, or that the Devonian *Acervulariæ* (so-called) hold to *Cyathophyllum*.

Axophyllum, again, comprises simple Clisiophylloid corals of Carboniferous age, in which there is a large vesicular pseudocolumella piercing a central tabulate area, which is enclosed by an accessory wall, and is in turn surrounded by a vesicular zone. Lastly, we may include here the Carboniferous genus *Lonsdaleia* (fig. 134), in which there is a composite, fasciculate, or astræiform corallum. Each corallite has, as usual in this family, a large pseudocolumella, formed of twisted lamellæ, and having a vesicular structure (fig. 171, A). The columella traverses a well-developed tabulate area, but the genus differs from the other types of the family in the fact that the outer zone of the corallum is occupied wholly by large lenticular vesicles, the septa being here obsolete, and being developed in the central region only. In the series of the *Clisiophyllidæ*, *Lonsdaleia* holds the place occupied by *Lithostrotion* in the series of the *Cyathophyllidæ*.

II. Zaphrentoidea.

The section of the *Zaphrentoidea* comprises those Rugose Corals in which there is a comparatively limited amount of dissepimental endotheca, the visceral chamber never being sheathed with a zone

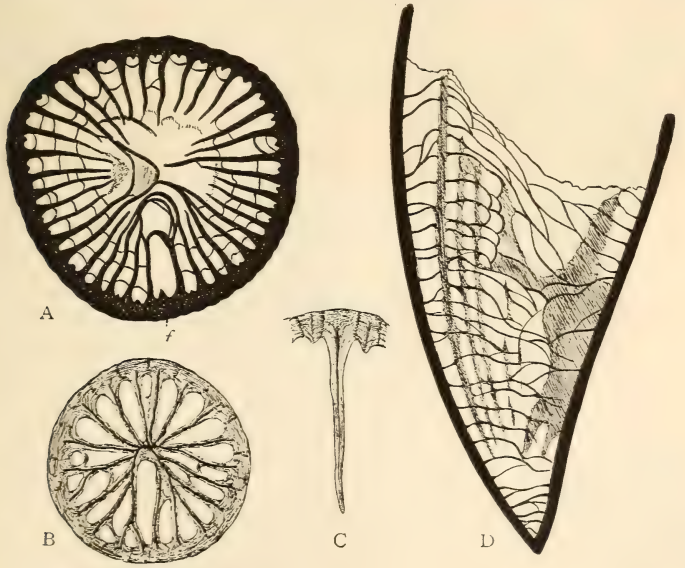


Fig. 172.—Morphology of *Zaphrentis*. A, Transverse section of a fully-grown individual of *Zaphrentis Enniskilleni*, from the Carboniferous Limestone, enlarged about twice. B, Transverse section of a very young example of the same, enlarged six times. C, Part of the theca of the same, enlarged, showing one long and two short septa, the bases of these structures forming the wall. The septa have a primordial lamina thickened by stereoplasma. D, Long section of the same, showing the tabulæ. (Original.)

of vesicular tissue; while there is, on the other hand, a proportionately extensive development of the tabulæ. [In the *Hadrophyllidæ*

and in *Palæocyclus porpita*, the corallum is so short that neither dissepiments nor tabulæ are developed at all.] The septa are thickened with stereoplasma (fig. 127, B and C), and are not "carinate." As a rule, the septa are of two orders, alternately long and short. In all the typical members of the section, the symmetry is conspicuously bilateral, and a tetrameral disposition of the septa can usually be readily determined. There is generally a well-marked fossula (fig. 172, *f*), placed dorsally and containing the "cardinal septum"; or ventral in position, enclosing the "counter septum"; or rarely lateral and traversed by one of the "alar septa." In some forms a fossula is not determinable (*e.g.*, in some species of *Streptelasma* and in *Lindstrœmia* generally). In the genera just mentioned it is also usual for the lower part of the visceral chamber to be more or less largely filled up with a deposit of stereoplasma. The Zaphrentoid Corals are exclusively Palæozoic, and range from the Ordovician to the Carboniferous period, or, if the genus *Polycœlia* be admitted here, to the Permian.

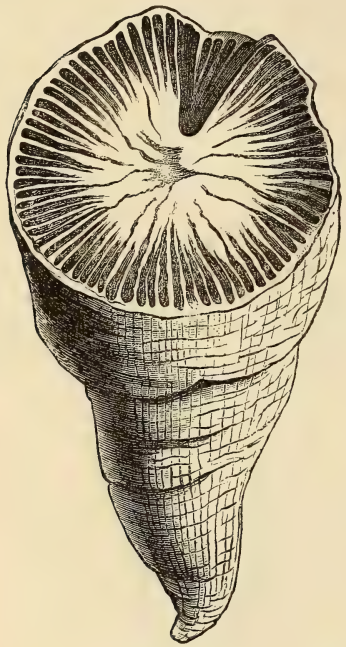


Fig. 173.—*Zaphrentis cornicula*, the walls of the calice broken away, and showing the "fossula," of the natural size. Devonian, America. (Original.)

Family 1. *Zaphrentidæ*.—The typical family of the Zaphrentoid Corals is that of the *Zaphrentidæ*, of which the genus *Zaphrentis* itself is the central form. The family is characterised by the marked bilaterality of the corallum, a well-developed fossula being present, while the development of the septa is usually characterised by the inequality in size of certain of these structures. The septum which occupies the fossula may be either the "cardinal septum" or the "counter septum," but in either case it is shorter than the other long septa. Neither a true columella nor a pseudocolumella are developed, and there is a thick theca formed by the coalescence of outgrowths from the outer ends of the septa (fig. 172, C). It is doubtful if a true epitheca is present.

Only the more important of the genera of the *Zaphrentidæ* can be here noticed, the chief being *Zaphrentis* itself. In this genus (fig. 173) the

corallum is simple, conical, turbinate, or cylindrical in form, more or less curved, and showing a conspicuous fossula in the obliquely placed calice. The fossula in different species is on the convex side of the corallum ("dorsal"), or on the concave side ("ventral"), or in rare cases is lateral. The septum included therein is usually very short (fig. 172, A and B), and may be obsolete, while more or fewer of the septa on each side generally bend round, and, partly coalescing, enclose the wide inner end of the fossular groove. The septa are moderately numerous, alternately long and short, the latter being commonly rudimentary and sometimes partly obsolete. The long septa extend a considerable distance inwards towards the centre of the visceral chamber, and often show a tendency to coalesce in groups. Dissepiments are sparingly developed in the outer zone of the corallum, but tabulæ are largely developed, and pass from side to side of the visceral chamber (fig. 172, D), often becoming united to form large arched vesicles. The species of *Zaphrentis* are mainly Carboniferous and Devonian, but some forms referred to the genus are Silurian.

The Devonian and Carboniferous genus *Amplexus* is closely similar to *Zaphrentis*, but the simple corallum is usually cylindrical in form, while the septa are much less perfectly developed, being confined to the margin of the visceral chamber, and thus leaving exposed a large central space occupied by nearly horizontal, complete tabulæ.

In the Carboniferous genus *Lophophyllum* there is a simple conical corallum of small size (fig. 174), which agrees with *Zaphrentis* in the scanty development of dissepiments and the possession of complete arched tabulæ. There is also a small fossula, which lodges the "cardinal septum" (fig. 174, B, *h*), this being shorter than the other septa. On the

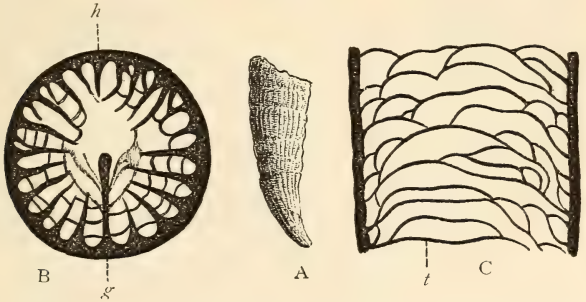


Fig. 174.—Structure of *Lophophyllum eruca*, from the Carboniferous Limestone, Scotland. A, Side-view of the corallum, enlarged slightly; B, Transverse section of the same, enlarged four times; C, Longitudinal section of the same, similarly enlarged. *h*, Cardinal septum; *g*, Counter septum; *t*, Tabulæ. (Original.)

other hand, the "counter septum" (fig. 172, B, *g*) is greatly developed, being much longer than the other septa, and having its inner extremity swollen. This enlarged septum has been regarded as a true columella, but an examination of very young specimens shows that its real nature is as just described. The remaining septa are unequal in size, but a division into alternately long and short septa cannot be recognised.

In the Carboniferous genus *Menophyllum*, again, there are three fossulæ, the largest being on the dorsal side of the corallum, and lodging the "cardinal septum," while the other two are lateral and lodge the

"alar septa," the tabulate area in the floor of the calice thus assuming the form of a half-moon. Lastly, in the Devonian genus *Anisophyllum* (fig. 175), the cardinal and alar septa are specially developed, and form three prominent ridges in the cup of the calice.

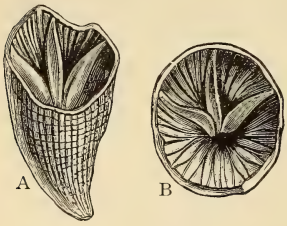


Fig. 175.—A, *Anisophyllum Agassizi*, slightly enlarged; B, Calice of the same, viewed from above—Devonian. (After Milne-Edwards and Haime.)

Outside of the typical family of the *Zaphrentidæ* are various Zaphrentoid corals which in the present state of our knowledge can only provisionally be arranged in groups, and the true affinities of which are not always clear. One group of forms, which may be provisionally spoken of as that of the *Hadrophyllidæ*, comprises certain singular little discoid corals for which the genera *Hadrophyllum*, *Baryphyllum*, *Combophyllum*, and *Microcyclus* (fig. 176) have been founded. In these singular types the simple corallum has the form of a flattened disc, the calice being so shallow as hardly to deserve the name, while the base is also often flat, the corallum thus becoming coin-shaped. There is generally a marked septal fossula, and the symmetry is conspicuously bilateral. The septa are smooth-edged, and irregular in

Fig. 176.—*Microcyclus discus*, from the Devonian (Hamilton Group) of North America. A, Upper surface of the corallum; B, Under surface of the same. The cross shows the natural size of the corallum. (Original.)

length, and the interseptal loculi are filled up with stereoplasma, no dissepiments nor tabulæ being developed. All the types of this group, so far as is certainly known, are found in rocks of Devonian age.

The type of a second group (*Palæocyclidæ*) is constituted by the singular *Palæocyclus porpita* (fig. 177) of the Silurian rocks of Gotland.[1] The corallum in this form is discoidal, the flat circular base being covered with a concentrically striated basal plate. The septa are forty-four, or rarely forty, in number, alternately long and short, the "cardinal septum" being shorter than the other septa, and being placed in a well-marked "fossula" (figs. 158, and 177, A), the symmetry thus becoming bilateral. The "counter septum" is not specially developed. All the septa are tuberculated and have crenulated edges. There are no dissepiments nor tabulæ, but the interseptal loculi are not filled up with stereoplasma. In this respect, as also in the crenulated form and more regular develop-

[1] *Palæocyclus porpita* certainly occurs also in the Wenlock Limestone of Britain (Dudley), but the *P. Fletcheri* of the same formation does not appear to be properly referable to the genus *Palæocyclus*, but belongs to *Pholidophyllum*.

ment of the septa, *Palæocyclus porpita* differs from the group of which *Hadrophyllum* is the type. The affinities of *Palæocyclus* cannot be regarded as clearly established. It is possible that the genus, instead of being placed here, should be looked upon as holding the same

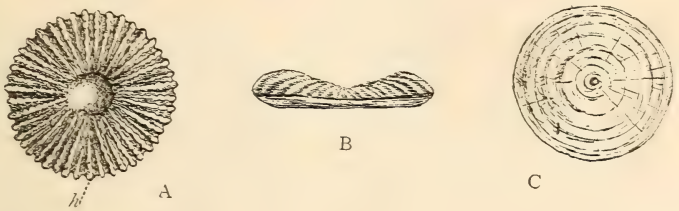


Fig. 177.—*Palæocyclus porpita*, from the Wenlock Limestone of Gotland. A, Upper surface (calice) of the corallum, showing the cardinal septum in the fossula (*h*); B, Side-view of the corallum; C, View of the flat under side of the corallum, with the concentrically striated epitheca. All the figures are enlarged about twice. (Original.)

position to the *Heliophyllidæ* that *Hadrophyllum* and its allies do to the *Zaphrentidæ*.

The genus *Streptelasma* may be regarded as the type of another group of Zaphrentoid Corals, to which the name *Streptelasmidæ* may be given. The corallum in this genus is simple and turbinate or conical in form. A true "theca" does not seem to be present, but the septa become much

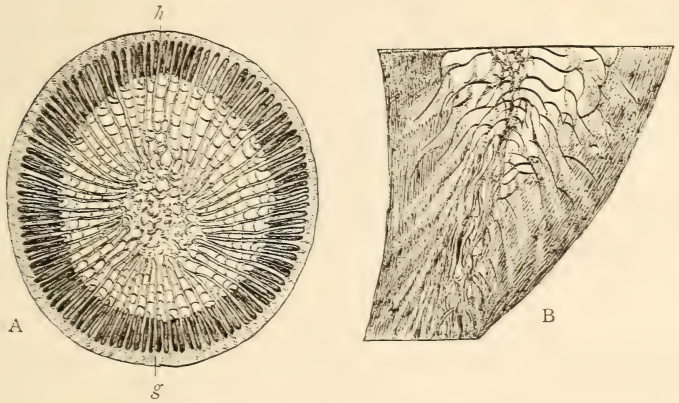


Fig. 178.—Structure of *Streptelasma corniculum*, from the Ordovician rocks (Cincinnati Group) of North America. A, Transverse section; B, Longitudinal section of the corallum, enlarged twice. The transverse section shows the thick false wall formed by the fusion of the outer portions of the septa. *h*, Cardinal septum situated in the fossula; *g*, Counter septum. In the specimen figured there are one hundred and eight septa, alternately long and short. (Original.)

thickened towards their outer edges, being fused with one another by their lateral margins for a considerable distance, and thus giving rise to a dense false wall (figs. 127, B and 178, A). The septa are numerous, of two orders, alternately long and short, the latter being buried for the greater portion of their length in the false wall. The symmetry is distinctly bi-

lateral, the cardinal and alar septa being clearly recognisable, in well-preserved specimens, by the pinnate arrangement of the costal furrows on the exterior of the corallum (fig. 156). The cardinal septum is reduced in size, and usually occupies the centre of a large fossula (fig. 178, A), but in some species (*e.g.*, in *S. europæum*) a fossula is wanting. The lower part of the visceral chamber is more or less extensively filled up with stereoplasma, and the upper part of the same is crossed by irregular tabulæ, dissepiments being also developed in moderate numbers. The centre of the visceral chamber is occupied by a large, irregularly reticulated or trabecular pseudocolumella (fig. 178, A), with which the inner ends of the long septa are directly connected, and which is highly characteristic of the genus. The species of *Streptelasma* are mainly Ordovician, but Silurian forms have also been recorded. The genus *Ptychophyllum* (if judged by the structure of the mushroom-shaped *P. patellatum* of the Silurian rocks) is very closely related to *Streptelasma*, the principal difference being that in this case the pseudocolumella is produced by a twisting together of the thickened inner ends of the longer septa. If, as maintained by Lindström, these two genera are to be regarded as identical, the name of *Ptychophyllum* will have to be suppressed in favour of the older title of *Streptelasma*.

Fig. 179.—*Lindstræmia Dalmani.* A portion of top of the theca is broken, in order to show the interior of the calice. Silurian.

Lastly, we may possibly place among the *Zaphrentoidea* the small, simple Palæozoic corals which constitute the genus *Lindstræmia* (fig. 179). These forms agree with the typical *Rugosa* in the pinnate arrangement of the septa and the resulting bilateral symmetry of the corallum, but they do not appear to possess a fossula. The distinctive feature in the genus is the fusion of the septa by their inner ends to form a sort of pseudocolumella, which is often of great size and projects into the floor of the calice. The lower portion of the visceral chamber is more or less extensively filled up by stereoplasma, but dissepiments and tabulæ are scantily developed in its upper portion. The species of *Lindstræmia* are mostly Ordovician and Silurian, but the genus survives into the Carboniferous period.

III. Cystiphylloidea.

The section of the *Cystiphylloidea* comprises those Rugose Corals in which endothecal tissue in the form of dissepiments is in general extensively developed, while tabulæ are absent or are incompletely developed, and the septa are more or less imperfect, and may be reduced to mere marginal striæ. When the septa are so far developed as to enable this point to be determined, it can be shown that the symmetry of the corallum is distinctly bilateral, and in some cases a well-marked fossula is present. The Cystiphylloid corals are wholly Palæozoic, and are confined to the Silurian and Devonian rocks.

Family 1. *Cystiphyllidæ.*—This is the typical family of the Cysti-

phylloid corals, and is characterised by the fact that the endothecal structures are more or less completely reduced to a vesicular tissue, composed of lenticular cells, which are often of specially large size in the centre of the visceral chamber, and in this region represent

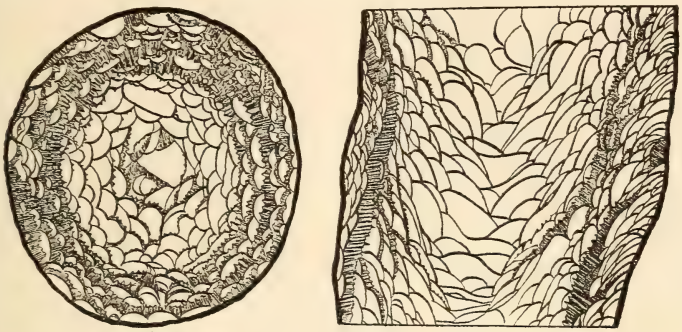


Fig. 180.—Structure of *Cystiphyllum cylindricum*, Lonsd., from the Wenlock Limestone of Ironbridge. A, Transverse section, enlarged twice; B, Part of a vertical section, similarly enlarged. (Original.)

tabulæ (fig. 180). The septa are rudimentary, but are usually recognisable as more or less distinct striæ or ridges on the surface of the calice.

The type-genus of this family is *Cystiphyllum* itself, in which the corallum is almost invariably simple (it is composite in the *C. fruticosum* of the American Devonian rocks), and is usually conical in form (fig. 181), though in some cases greatly flattened. The wall is well developed, and the visceral chamber is entirely filled with a vesicular tissue of obliquely disposed lenticular cells, which in the central region of the corallum often show a well-marked arrangement in funnel-shaped layers. The calice sometimes exhibits nothing but the rounded upper surfaces of the lenticular vesicles just spoken of, but its surface commonly shows more or less marked radial ridges or radiating rows of tubercles, which represent the septa. In some cases, as in the Devonian *C. sulcatum* and *C. lamellosum*, a well-marked dorsal fossula is present; and in the latter species it is sometimes even possible to recognise a disposition of the septal ridges in four groups, corresponding with the four quadrants of a typical Rugose Coral. All the known species of *Cystiphyllum* are found in the Silurian or Devonian rocks, one of the commonest species being the *C. vesiculosum* (fig. 181) of the Devonian rocks of North America and Europe. Through *Actinocystis* a transition can without violence be effected between the genus *Cystiphyllum* on the one hand and *Cyathophyllum* on the other hand.

Family 2. *Calceolidæ*. — This family has been founded for a number of remarkable Palæozoic corals, of which the principal genera are *Goniophyllum*, *Rhizophyllum*, *Aræopoma*, and *Calceola*. The corallum in this family is simple and conical in form, very

commonly more or less angulated, and assuming a pyramidal or quadrilateral figure. Internally, the structure may not differ essentially from that of *Cystiphyllum*, the visceral chamber being filled with an endothecal vesicular tissue, and the septa being incomplete or rudimentary (fig. 182, B). Sometimes the septa are obsolete, but they are usually recognisable as radiating ridges or rows of tubercles in the calice, or they may even form radiating lamellæ which intersect the marginal region of the visceral chamber. The essential character of the family, however, is found in the fact that the calice is closed by a variously constructed lid or "operculum," composed of one or more pieces (fig. 182, A). In this feature, the corals of the present family differ from all recent Madreporarians, though a species of operculum is found in some living Alcyonarians (*Primnoa* and *Paramuricea*). The structure and affinities of the family of the Operculate Corals have been admirably worked out by Lindström; and all the known genera of the family are Silurian or Devonian.

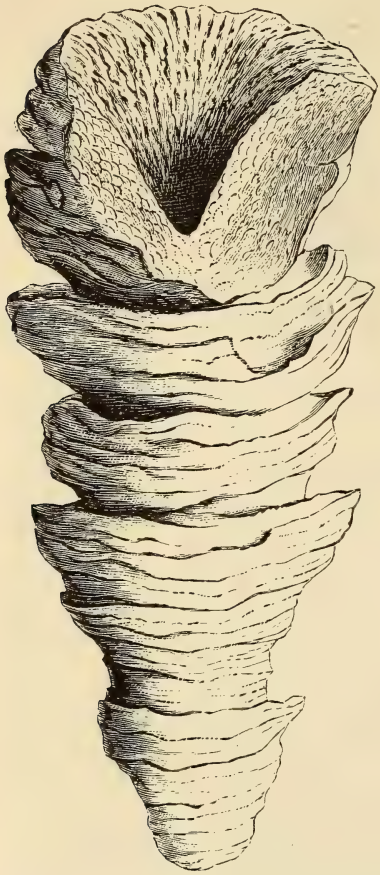
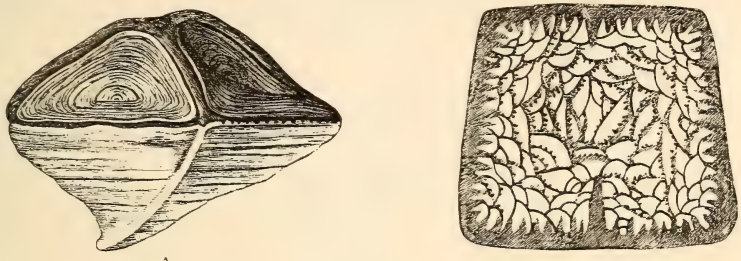


Fig. 181.—*Cystiphyllum vesiculosum*, showing "rejuvenescence," the corallum consisting of a succession of cups produced by budding from the original polype. One side of the calice is broken away, and shows the internal structure. Of the natural size. Devonian, America and Europe. (Original.)

In the Silurian *Goniophyllum* (fig. 182) the corallum is distinctly quadrilateral, its four sides being flattened. The internal structure is wholly vesicular, the cells of the central region of the visceral chamber being of large size and representing tabulæ. The quadrangular calice is deep, and is furnished with marked septal ridges, of which four—one in the middle of each side—are specially prominent, the longest being the "cardinal septum," while the other three are the "counter" and "alar" septa. The septa are not mere calicine striæ, but are truly lamellar, though they are marginal. The calice is closed with

an operculum of four calcareous plates, of which the dorsal and ventral ones are trapezoidal and the lateral ones are triangular.

In *Rhizophyllum* the conical or pyramidal corallum is attached to foreign objects by root-like exothecal processes developed from its flattened under surface, the upper surface being rounded. The calice has septal striæ and a distinct fossula, the internal structure is wholly of



A B

Fig. 182.—A, *Goniophyllum pyramidale*, from the Silurian of Gotland, showing the operculum in place, twice the natural size; B, Transverse section of the same species, slightly enlarged. (A is after Lindström; B is original.)

oblique vesicles, and the operculum is in the form of a single semicircular plate. The species of the genus are mostly Silurian, but one form is found in the Lower Devonian.

Still more closely allied to *Cystiphyllum* is the genus *Aræopoma*, comprising only the *A.* (*Cystiphyllum*) *prismaticum* of the Silurian rocks. The corallum in this form is subangular, more or less clearly four-sided, the calice having radial rows of septal tubercles, and the surface exhibiting distinct rugæ. Internally the structure is wholly vesicular, and the calice is closed by an operculum of subtriangular valves.

Lastly, in the genus *Calceola* (fig. 183), the slipper-shaped corallum is free, and has the form of a slightly curved four-sided pyramid, of which one side is broad and flat, the opposite side being equally broad but convex, while the lateral faces are much reduced, and are only represented by the rounded junctions of the two broad faces. The calice is deep, corresponding in form to the exterior, and marked internally with distinct septal striæ. The "cardinal septum" is clearly marked, and is placed in the centre of the vaulted side of the corallum, sometimes in a distinct groove or fossula, while the septa on both sides of this have a pinnate arrangement. The "counter septum" is in the middle of the flat side of the corallum, and is also often in a distinct fossula. The calice is closed by a half-moon-shaped operculum, which resembles the valve of a Brachiopod in form and sculpturing, its under surface, however, showing a prominent median and fainter lateral septal ridges. The internal structure is dense, the thick wall apparently solid, but showing, according to the observations of Kunth, a finely vesicular structure. The only known species of this genus is the *Calceola sandalina* of the Middle Devonian rocks, an abundant and characteristic fossil in

Fig. 183.—The corallum of *Calceola sandalina* (a small example), from the Middle Devonian of Gerolstein, viewed from its rounded side, of the natural size.

strata of this age in Europe. It may be noted in connection with *Calceola sandalina* that the internal structure of the curious *Cystiphyllum lamellosum* of the same geological horizon exhibits, in its young stages, a curious resemblance to that of the present form, the latter, however, not being known to possess an operculum. This fact, along with the general identity in structure between *Arœopoma prismaticum* and the typical *Cystiphylla*, may be taken as fully corroborating Lindström's conclusion that these remarkable Operculate Corals cannot be separated from the *Madreporaria Rugosa*.

CHAPTER XIX.

ZOANTHARIA—continued.

MADREPORARIA FUNGIDA AND PERFORATA.

SECTION III. MADREPORARIA FUNGIDA.

This section includes simple or composite Madreporarians, in which the interseptal loculi are crossed by trellis-like calcareous bars ("synapticula"). In the composite forms, where adjacent corallites are connected by prolongations of their septa ("septo-costæ"), the interspaces between these prolongations are also synapticulate. The septa are lamellar, and are usually solid, though occasionally perforations exist. When there is a basal plate it is usually perforated by apertures, but it may be imperforate. Endothecal structures (dissepiments and columella) may or may not be developed. Tentacles in the living forms "short, lobe-like, scattered, sometimes obsolete" (Duncan).

So far as certainly known, the section of the *Madreporaria Fungida* has no Palæozoic representatives; but the Secondary and Tertiary deposits have yielded a large number of fossil forms, only a few of the more important of which can be alluded to here.

By Professor Martin Duncan the section of the *Fungida* is divided into the following five families:—

Family 1. *Plesiofungidæ*.—This family is related to the *Aporosa*, and comprises simple or composite *Fungida*, in which dissepiments exist in addition to the synapticula, and the septa are usually solid and imperforate. The principal genus in this family is *Thamnastræa*, including a large number of species, which range from the Trias to the Miocene Tertiary, and have a very wide geographical distribution. In this genus the corallum is composite and is usually massive or lobate in form, sometimes laminar or encrusting; while the corallites have ill-defined walls. The calices (fig. 184, A) have distinct centres, but are shallow, and the septa become con-

fluent with those of neighbouring cups by means of septo-costal prolongations. The septa appear to be sometimes perforated, sometimes imperforate (Duncan), and both dissepiments and synapticula are developed, a variably shaped columella being also

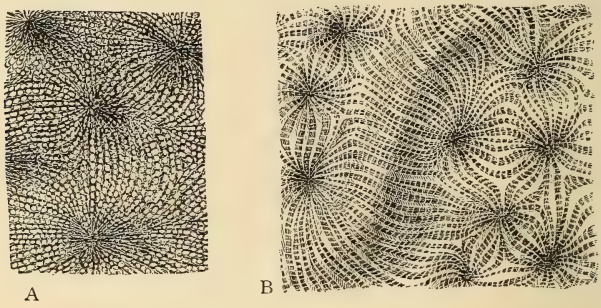


Fig. 184.—A, Surface of *Thamnastræa agaricites*, from the Cretaceous deposits of Gosau; B, Surface of *Comoseris conferta*, from the Oligocene Tertiary of Vicenza, enlarged twice. (After Zittel.)

present. Closely allied to *Thamnastræa* is the Jurassic genus *Clausastræa*.

Family 2. *Fungidæ*.—In the true *Fungidæ* the corallum is simple or compound, the interseptal loculi showing numerous synapticula, but there being no dissepiments. The septa are usually imperforate, and the basal wall is generally perforated. As restricted by Duncan, this family comprises no other fossil genus than the *Micrabacia* of the Cretaceous rocks. In this genus the corallum is of small size, free and unattached, of lenticular form, with a convex base covered with a perforated basal plate.

Family 3. *Lophoseridæ*.—In this family the corallum may be simple or compound, the wall being imperforate, and the septa also usually solid. There are synapticula, but no dissepiments. The simple forms of this family may be turbinate, discoid, or attached by a wide base, and are represented in Secondary and Tertiary deposits by various generic types (*Trochoseris*, *Cycloseris*, *Podoseris*, &c.) The composite types have their calices united by confluence of the septo-costæ, and usually possess a thin laminar or frond-like corallum. Besides such recent genera as *Lophoseris* and *Mycedium*, we have here a number of fossil types, some of which (such as *Protoseris* and *Comoseris*, fig. 184, B) are found in rocks as ancient as the Jurassic.

Family 4. *Anabacidæ*.—This small family includes only the two genera *Anabacia* and *Genabacia*, the former being simple and the latter composite, and both being confined to the Jurassic rocks. The septa in these genera are perforated, and the wall is indistinct,

while there are synapticula but no dissepiments. *Anabacia* is discoid in form, and of small size, and its basal wall is wanting.

Family 5. *Diesioporitidæ*.—This family includes *Fungida* in which the septa are trabeculate and the septa regularly porous, thus approaching the *Madreporaria Perforata*. When a wall is present, it is imperforate. Synapticula are present, and dissepiments may or may not exist. Most of the genera included in this family (*Lepto-*

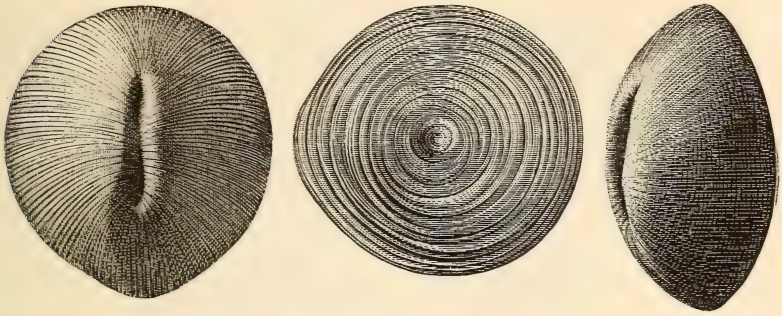


Fig. 185.—*Cyclolites elliptica*, viewed from above, rom below, and from the side. Cretaceous.

phyllia, *Cyclolites*, *Microsolena*, &c.) are Jurassic or Cretaceous, the well-known genus *Cyclolites* occurring in both of these formations. In this genus (fig. 185), the corallum is simple and free, discoid, with a flat or slightly concave base, and either circular or elliptical in outline. The under surface of the corallum is covered with a well-developed, concentrically striated basal plate. The septa are trabecular and more or less perforated, and there is either no columella or a rudimentary one.

Forming a transition between the typical *Fungida* and the typical *Perforata* is the Jurassic genus *Microsolena* (fig. 186), in which the corallum is massive, of variable shape, but usually more or less lobed. The basal wall is covered with a strong epitheca, and the calices are not circumscribed by a definite wall. The septa are trabecular and perforated, and synapticula are abundantly developed.

Fig. 186.—Fragment of *Microsolena ramosa*, and three of the calices of the same enlarged. Jurassic.

Section IV. Madreporaria Perforata.

This section includes simple or composite Madreporarians in which the calcareous tissue (sclerenchyma) of the corallum is more or less conspicuously porous or reticulate (fig. 187, c); the visceral chambers of the corallites being thus placed, in the compound forms, in communication with one another. The septa may be solid, but are usually more or less porous, being often represented by irregular trabeculæ, or, in other cases, by rows of calcareous spines. Dissepiments are usually present, and tabulæ are commonly developed. The existing *Madreporaria Perforata* fall into the three groups of the *Eupsammidæ*, *Madreporidæ*, and *Poritidæ*, while we may place here the three extinct groups of the *Favositidæ*, *Syringoporidæ*, and *Thecidæ*. These three last-mentioned groups

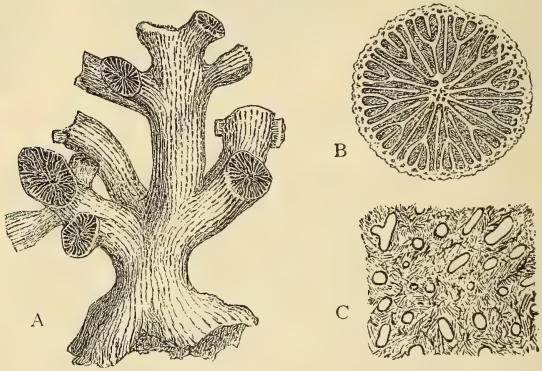


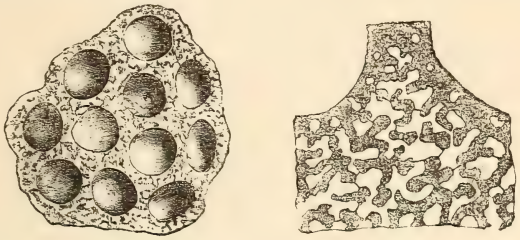
Fig. 187.—A, *Dendrophyllia elegans*, from the Oligocene Tertiary of Brockenhurst, of the natural size; B, Transverse section of the same, enlarged (after Zittel); C, Portion of a section of a recent species of *Dendrophyllia*, showing the porous structure of the skeleton.

are essentially Palæozoic, the *Favositidæ* alone having any Mesozoic representative (the *Koninckia* of the Cretaceous rocks). Of the three existing groups of the *Perforata*, the *Poritidæ* appear to be the most ancient, the Ordovician genus *Protarœa* belonging to this family, while the *Calapœcia* (*Columnopora*) of the same formation links the *Poritidæ* with the *Favositidæ*. The Devonian genera *Arœopora* and *Cleistopora*, and the Carboniferous genus *Palœacis* (fig. 188) may also be referred to the *Poritidæ*. The *Eupsammidæ* are also an ancient group, being represented in the Silurian rocks by the genus *Calostylis*. On the other hand, the *Madreporidæ* are of comparatively modern origin, the first known types appearing in the Tertiary deposits. Upon the whole, however, the existing groups of the *Eupsammidæ*, *Poritidæ*, and *Madreporidæ* do not present

themselves in any prominent manner till the Tertiary period is reached, and they have attained their maximum at the present day.

In the following brief summary of the characters and distribution in time of the leading groups of the Perforate Madreporarians, it will be best to take first the three recent families above mentioned.

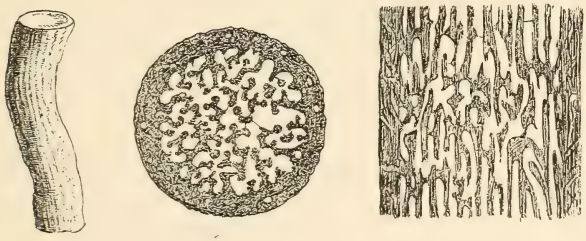
Family 1. *Eupsammidæ.*—In this family the corallum may be simple or compound, the *wall* of the corallites being perforated, while



A B

Fig. 188.—*Palæacis cyclostoma*, from the Carboniferous rocks of Scotland. A, Upper surface of a colony enlarged twice; B, Vertical section of the corallum, showing the reticulated structure of the skeleton, enlarged. (Original.)

the principal septa may be entire and imperforate. The smaller septa are, however, usually perforate, and in other cases all the septa are trabecular. There is a limited development of endothecal tissue, the interseptal loculi thus remaining more or less open. This family is principally Tertiary and Recent, but the genus *Calostylis* is Silurian, and there are also Cretaceous types (*Stephanophyllia*, &c.)



A B C

Fig. 189.—*Calostylis Andersoni*, from the Wenlock Limestone of Shropshire. A, A broken specimen, enlarged slightly; B, Transverse section, enlarged five times; C, Vertical section, similarly enlarged, showing the thick wall and the trabecular character of the septa. (Original.)

It is clear, therefore, that our knowledge of the past history of the family is extremely imperfect.

The most ancient type of this family is the genus *Calostylis*, first described by Lindström from the Wenlock Limestone of Gotland, but occurring also in deposits of the same age in Britain. In this genus the

corallum (fig. 189) is cylindrical, and may be simple, or may become composite by the production of lateral buds. The wall is thick and porous, but is covered here and there with a thin striated epitheca. The septa are so highly perforated as to become more or less trabecular (fig. 189, B and C), and they may unite centrally to form a species of spongy columella; but dissepiments are very imperfectly developed. There is no reason to doubt the correctness of Lindström's reference of *Calostylis* to the *Eupsammidæ*, with which the genus agrees in all essential characters. No type of the *Eupsammidæ* has hitherto been detected in any Palæozoic deposit of later age than the Silurian, nor in any of the older Mesozoic rock-groups; but in the Cretaceous rocks we meet with the genus *Stephanophyllia*. In this genus the corallum is free, simple, and discoid, with an open circular calice; and species of the genus range from the Cretaceous to the present day. In *Balanophyllia*, ranging from the Eocene Tertiary to the present day, the corallum is also simple, but is usually permanently fixed to some foreign body. An allied type is the Pliocene and Recent genus *Thecopsammia*, which is considered by Professor Martin Duncan to be related in some respects to the Silurian genus *Calostylis*. Also allied to *Balanophyllia* is the Eocene genus *Endopachys* (fig. 190), in which the corallum is simple and

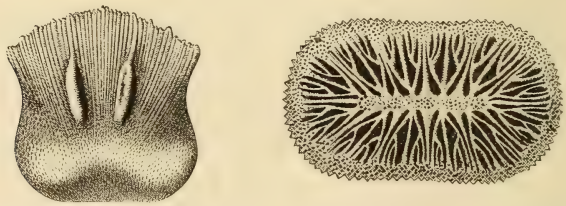


Fig. 190.—*Endopachys Maclurii*, viewed in profile and from above. Eocene Tertiary.

compressed, and a spongy columella is present, while the keeled base is continued into two wing-like expansions. The type of another group of the *Eupsammidæ* is the well-known genus *Dendrophyllia* (fig. 187), in which the corallum is composite and generally of a dendroid form, the corallites being cylindrical, and having a spongy columella. The species of *Dendrophyllia* range from the Eocene Tertiary to the present day.

Family 2. *Madreporidæ*.—In this family the corallum is invariably composite, the mode of increase being by gemmation, and the constituent corallites of the colony being united by an abundant spongy cœnenchyma. The corallites have porous walls, which are not distinct from the cœnenchyma, and the septa are usually fairly developed, and are lamellar. The interseptal loculi have dissepiments, but a columella is wanting. As here defined, the family of the *Madeporidæ* includes only the single genus *Madrepora*, including a vast number of forms, ranging in time from the Eocene Tertiary to the present day. The corallum (fig. 191) in this genus is very variable in shape, being most usually branched or tufted; the corallites are tubular, with more or less projecting calices; and the visceral cham-

ber is divided into two halves by two of the six principal septa, which are specially developed, and nearly meet along their inner edges.

Family 3. *Poritidæ*.—In this extensive family the corallum is always composite, the constituent corallites being united directly or by the intervention of a more or less copious cœnenchyma. In either case the calcareous tissue of the corallum is spongy or reticulate, and the porous walls of the corallites are mostly not separable from the

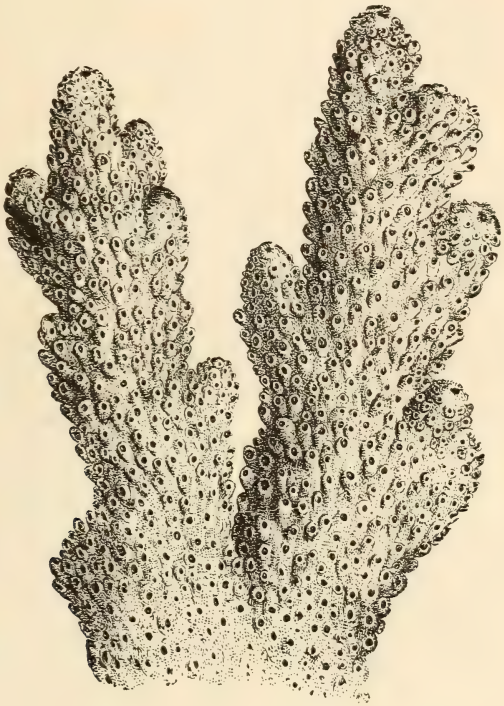


Fig. 191.—*Madrepora plantaginea*, of the natural size, showing the porous cœnenchyma and the tubular corallites. Recent.

cœnenchyma, when this latter exists. The septa may be rudimentary or obsolete, but they are usually present, and have the form of vertical rows of spinules, which often anastomose, and give rise to a sort of trellis-work. Rarely, the septa are imperforate and lamellar. In some cases tabulæ are present, and a columella may or may not be developed. The oldest types of the *Poritidæ* appear in the Ordovician rocks, but the family is represented in the Palæozoic deposits by but a few isolated genera (*Protarœa*, *Arœopora*, *Palœacis*, &c.),

and is mainly Mesozoic and Tertiary, numerous forms existing at the present day.

The group of the *Poritidæ* which is most nearly allied to the *Madreporidæ* is that of which *Turbinaria* is the type, characterised by the fact that the corallites have distinct walls and are united by an abundant reticulate or spongy cœnenchyma. *Turbinaria* itself ranges from the Miocene Tertiary to the present day, and allied types are *Actinacis* (Cretaceous to Oligocene) and *Astræopora* (Eocene to Recent). More or less closely allied to the preceding are the little Carboniferous corals which constitute the genus *Palæacis*.[1] In this genus the corallum (fig. 188) is composed of short and wide corallites, united together directly or by the intervention of a limited amount of cœnenchyma. The tissue of the skeleton is more or less trabecular (fig. 188, B), and the septa are obsolete, being represented only by rows of granules in the interior of the deep calices. The species of *Palæacis* are found growing upon the stems of Crinoids and other foreign bodies in the Lower Carboniferous rocks of both Europe and North America.

The genus *Porites* is the type of another group of the *Poritidæ*, characterised by the reticulated sclerenchyma, the almost total or total absence of a cœnenchyma, and the generally trabecular septa. The species of

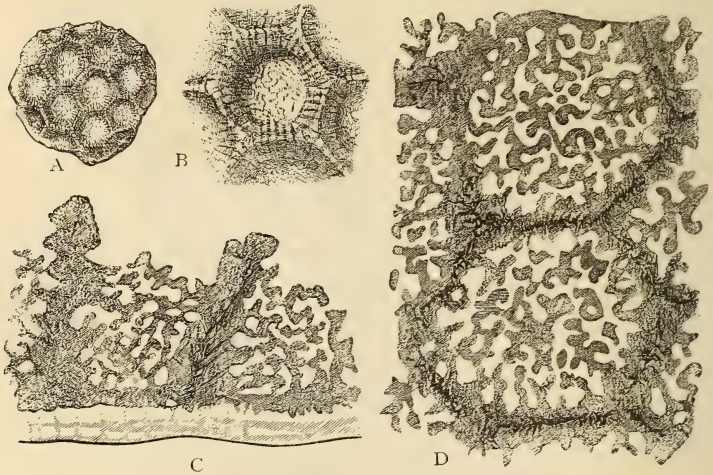


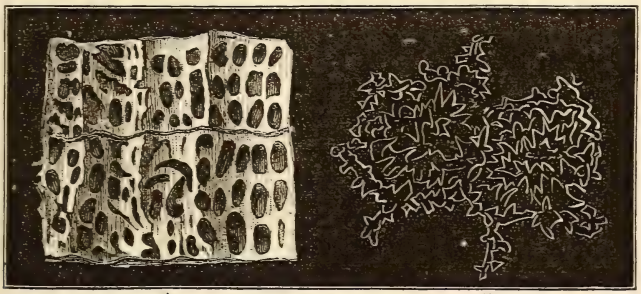
Fig. 192.—*Cleistopora geometrica*, Edw. & Haime, sp. A, Upper surface of a full-sized individual, of the natural size; B, A single calice enlarged; C, Vertical section of a specimen growing upon a Brachiopod, enlarged five times; D, Tangential section of the same specimen similarly enlarged. (Original.)

Porites are abundant at the present day, and are largely concerned with the building up of coral-reefs; while the earliest types of the genus occur in the Cretaceous rocks. Allied to *Porites* are various Tertiary

[1] Misled by certain peculiarities in the minute structure of the skeleton, the present writer was formerly induced to believe that *Palæacis* did not properly belong to the corals.

genera, such as *Litharæa*, *Rhodaræa*, &c. We may also place here the ancient genera *Stylaræa* and *Protaræa*, both of which commence in the Ordovician rocks, the latter surviving into the Devonian period. In the Devonian rocks we find, further, the singular genus *Cleistopora*, represented only by the little *C. geometrica* of the European Devonian rocks, in which the corallum (fig. 192, A) is composed of short polygonal corallites, forming a discoid colony which is usually attached by its under surface to some foreign body. The corallites are united by fusion of their walls, which are slightly porous, and the septa are only present as marginal striæ (fig. 192, B). The characteristic feature about the genus, however, is that the whole of the visceral chamber, below the calice, is filled with reticulated or trabecular calcareous tissue (fig. 192, C and D).

Lastly, a third group of the *Poritidæ* is typified by the genus *Alveopora*, the most characteristic feature of the group being that the walls of the corallites (fig. 193, A) are spongy and porous, while the septa (fig. 193, B) are trabecular, and well-developed tabulæ are usually present. The



A B

Fig. 193.—*Alveopora spongiosa*, one of the recent *Poritidæ* (after Dana). A, Some of the corallites cut vertically and enlarged, showing the tabulæ and the perforated walls; B, View of the calices from above, enlarged.

genus *Alveopora* itself ranges from the Eocene Tertiary to the present day, but the genus *Aræopora*, properly referred here by Waagen, is found in the Devonian deposits of Australia and the Carboniferous rocks of India. In this ancient type the corallum is massive, and is composed of polygonal corallites, which have their walls fused with one another. The walls are composed of spongy tissue, with irregular pores, the septa being trabecular or reticulate, while tabulæ may be more or less extensively developed. The Cretaceous genus *Koninckia*, though incompletely investigated, may also be placed here as a provisional arrangement; while the recent genus *Favositipora*, as described by Mr Saville Kent, would appear to form a connecting link between *Alveopora* and *Favosites*.

Family 4. *Favositidæ*.—This large and important family of Corals is characterised by the possession of a variably shaped corallum composed of polygonal or sub-cylindrical corallites, which are usually in close contact throughout their entire extent, but are not completely united by fusion of their walls. The walls of the corallites are porous, the visceral chambers of adjacent corallites

being thus placed in direct communication; but the perforations are not irregular, and are restricted to definite, circular or oval apertures known as "mural pores." There is no true cœnenchyma; and the condition of the septa is extremely variable, these structures being sometimes obsolete, sometimes in the form of marginal ridges, and most commonly in the form of vertically disposed rows of spinules. Tabulæ are usually well developed and complete, but

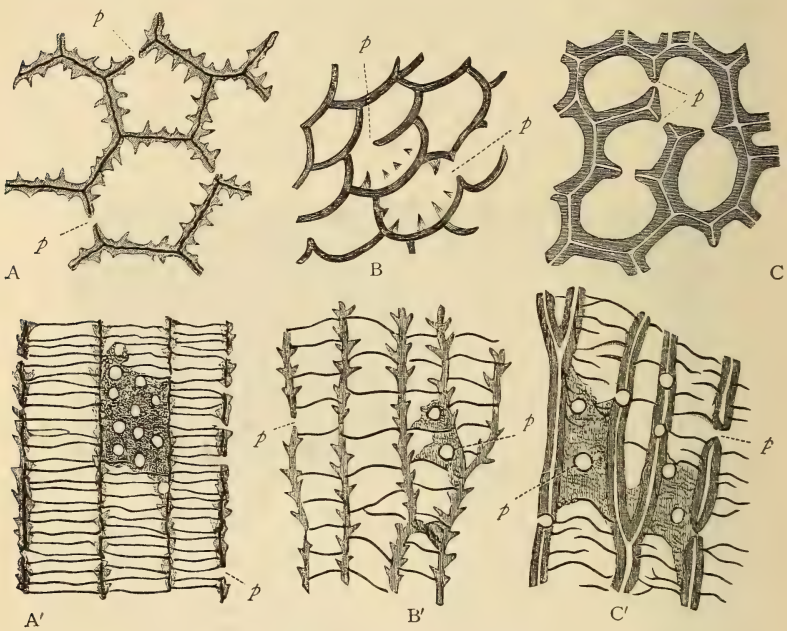


Fig. 194.—Thin sections of Favositoid Corals, showing the phenomena presented by the mural pores. A, Tangential section of *Favosites* sp., from the Devonian of Queensland, enlarged six times. A′, Vertical section of the same similarly enlarged; in two of the tubes the section traverses the centre of the visceral chambers, but in one it corresponds in part with the wall of the corallite. B and B′, Tangential and vertical sections of *Alveolites Labechei*, E. & H., from the Wenlock Limestone of Ironbridge, enlarged ten times. [The septal thorns which characterise this species, as also *A. battersbyi*, E. & H., are mostly omitted in the drawing.] C and C′, Tangential and vertical sections of *Pachypora* sp., from the Corniferous Limestone of the Falls of the Ohio, enlarged ten times. In all the figures the letter *p* indicates the mural pores. (Original.)

they are sometimes imperfect. The corallum increases by the form of budding which Waagen has defined as "inter-mural gemmation" (see p. 254).

The family of the *Favositidæ* is obviously allied to that of the *Poritidæ*, from which it is separated principally by the fact that the walls of adjacent corallites are not undistinguishably fused (though they may appear to be so in specimens in bad preservation), while the perforations in the walls are in the form of more or less definite

"mural pores." As here restricted, the family is exclusively Palæozoic in its range, the earliest known types appearing in the Ordovician, while the latest are found in the Carboniferous rocks. The great majority of forms, however, are Silurian and Devonian.

There are certain appearances in thin sections of the *Favositidæ*, as seen under the microscope, which it is desirable to understand. In the first place, the individual corallites of the colony have distinct walls. Hence, in thin sections (fig. 194, A and C), the partition which separates contiguous tubes usually exhibits a central dark or light line (the "primordial wall") bounded on each side by a layer of fibrous "stereoplasma." In badly preserved specimens it may not be possible to demonstrate the primordial mural plate in thin sections, but the real distinctness of the corallites is shown by the fact that in fractured examples the individual tubes commonly separate from one another along the line of this plate, each tube thus retaining its own proper wall.

In the second place, the so-called "mural pores" of the *Favositidæ* are rounded or oval apertures, usually arranged in longitudinal series, which perforate the walls of adjacent corallites and place adjoining visceral chambers in direct communication. They are sometimes not completed, since the thin "primordial wall" which separates contiguous tubes is sometimes not actually perforated. The mural pores are most regular in form and distribution in the genus *Favosites*, in which the pores are often surrounded by slightly raised margins, and are arranged in one or more series along the flat faces of the prismatic corallites (fig. 195, D). In such genera as *Pachypora*, where the corallites have greatly thickened walls, the mural pores assume the character of *tubes* rather than of mere *pores*, and in such cases they often perforate the walls in a tortuous manner. As regards their recognition in thin sections, mural pores appear in transverse sections of the tubes (fig. 194, A, B, C) as gaps or deficiencies in the wall forming the circumference of the corallite, the size of this gap depending on the size of the pores. In vertical sections (fig. 194, A′, B′, C′) the pores may similarly present themselves as gaps in the walls of the corallites. It very commonly happens, however, that a vertical section may in part *run along the actual wall* of the corallites, instead of merely dividing the tube longitudinally; and when this happens, the mural pores are seen as round or oval perforations in the wall within the space included between the lateral boundaries of the tubes.

The principal genus of the *Favositidæ* is *Favosites* (= *Calamopora*, Goldfuss) itself, the species of which range from the Ordovician to the Carboniferous inclusive. In this genus the corallum (fig. 195) is commonly massive and often of large size, but in other cases it may be lobate or branched. The corallites are numerous, usually more or less conspicuously polygonal, with thin and distinct walls. The mural pores are arranged in rows along the flat faces, or, more rarely, along the angles, of the prismatic corallites. In the former case, each face of the tube may carry one, two, or three rows of pores, this being, *generally*, a constant feature in different species. There are numerous tabulæ, and these structures are usually "complete" (*i.e.*, they stretch entirely across the visceral chamber); but

they may be "incomplete." In no instance are the tabulæ "cystoid"—that is to say, they do not anastomose so as to give rise to a vesicular tissue of arched cells. The septa in *Favosites* are sometimes wanting, but are usually represented by vertical rows of pointed tubercles or of slender calcareous spines. As previously mentioned, the tabulæ in some species of *Favosites* are "incom-

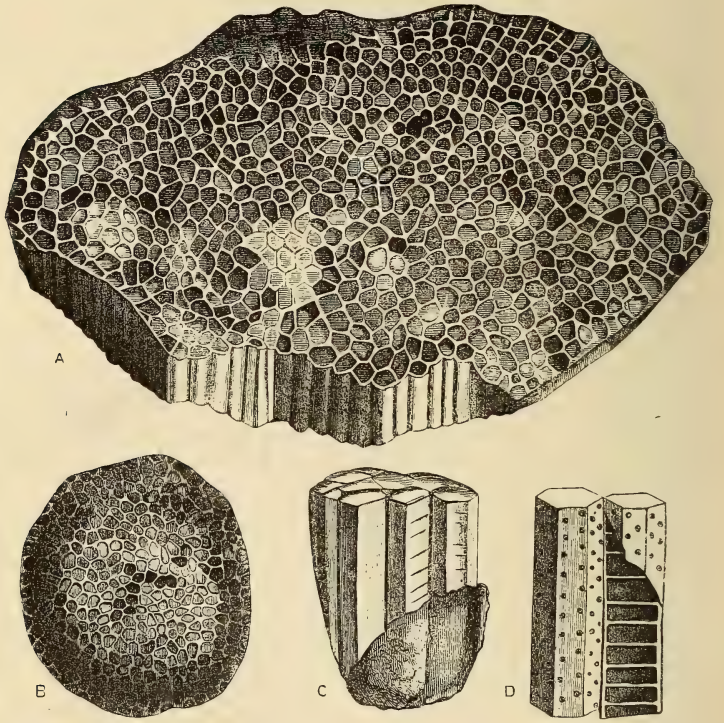


Fig. 195.—A, A specimen of *Favosites Gothlandica*, Lam., from the Niagara Limestone (Wenlock) of Owen Sound, Ontario, of the natural size; B, A small example of the same species from the Wenlock Limestone of Dudley, with comparatively minute corallites, of the natural size; C, Fragment of the same species, with large-sized corallites, from the Wenlock Limestone of Gotland, of the natural size; D, Part of two corallites of the same species, from the Corniferous Limestone (Devonian) of Woodstock, Ontario, slightly enlarged. (Original.)

plete," having the form, some or all of them, of thin, close-set transverse plates which only extend across about one-third or one-half of the diameter of the visceral chamber. This condition of the tabulæ is characteristic of such forms as the Devonian *F. hemispherica* (fig. 196), and the generic name of *Emmonsia* has been proposed for these.

Nearly allied to *Favosites* is the genus *Pachypora*, in which the

corallum is usually lobate or dendroid, and the corallites have their walls more or less extensively thickened by a secondary deposit of stereoplasma, the visceral chambers thus becoming more or less contracted, especially in the peripheral region of the colony (fig. 197).

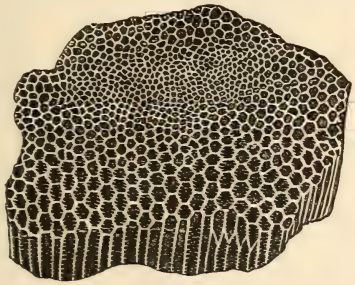


Fig. 196.—Fragment of *Favosites* (*Emmonsia*) *hemispherica*, of the natural size. Devonian, America. (After Billings.)

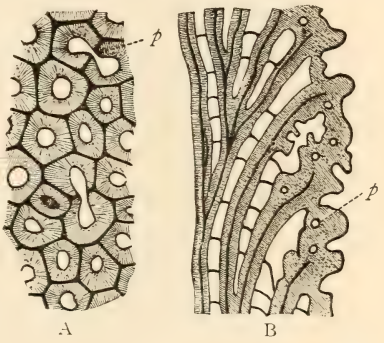


Fig. 197.—A, Transverse section of a few corallites of *Pachypora Nicholsoni*, Frech, from the Devonian of the Eifel, enlarged seven times, showing the thickened walls of the corallites; B, Vertical section of a few tubes of the same. *p*, Mural pores. (Original.)

The tabulæ in this genus are straight and complete; the septa are usually rudimentary; and the mural pores are generally large and uniserial, being converted into tubes in the more highly thickened portions of the corallites. The species of *Pachypora* are mostly Silurian and Devonian, but some forms appear to occur in the Carboniferous rocks. Closely related to *Pachypora* is the Silurian and Devonian genus *Striatopora* (fig. 198), in which the corallites also have greatly thickened walls, but the calices are surrounded by a cup-shaped thickened margin, the floor of which is striated by rudimentary septal ridges. Another allied type is the genus *Trachypora*, the species of which are principally Devonian. Here we may also place the curious Silurian genus *Laceripora*, in which the mural pores are uniserial and of large size, and the septa are in the form of marginal ridges.

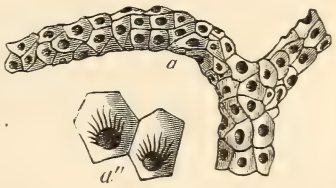


Fig. 198.—Fragment of *Striatopora flexuosa* of the natural size, and two calices enlarged. Silurian. (After Hall.)

The genus *Alveolites* is the type of another group of *Favositidæ* in which the corallites are usually more or less compressed, so as to appear triangular, or semilunar, or crescentic when transversely divided. The septa are usually present in the form of one, two,

or three elongated tooth-like ridges (fig. 199); but in some species the corallites possess strong ascending calcareous spines, the nature of which is different. The mural pores are uniserial and of large size, and the tabulæ are complete and more or less horizontal.

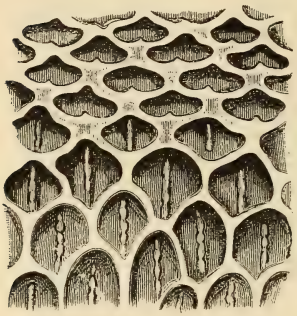


Fig. 199.—Calices of *Alveolites suborbicularis*, Lam., greatly enlarged, showing the single septal ridge. Devonian, Eifel. (After Goldfuss.)

The species of *Alveolites* usually have a branched or massive corallum, the latter usually formed of superimposed crusts; and they are found in the Silurian and Devonian deposits. An allied genus, with a similar geological range, is *Cœnites*, in which the corallites are greatly compressed, and are much thickened towards their mouths.

Another group is constituted by the genera *Pleurodictyum* and *Michelinia*, in both of which the tabulæ are more or less "cystoid" or vesicular, and the mural pores are very irregular. It is, indeed, very doubtful if these two genera can be separated, and in case of their union the name of *Michelinia* will have to be abandoned. In *Pleurodictyum* (fig. 200) the corallum is discoid; with a flat or concave base, covered with an epithecal plate, and attached at one point to a foreign body. The corallites are polygonal, and diverge from the centre of the base, those on the circumference being nearly horizontal or even bent downwards, while the median ones are more or less perpendicular. The mural pores are numerous and quite irregular; and in one species there is the singular feature that the mural pores of the under sides of the peripheral corallites pass directly through the basal plate of the colony, which thus becomes perforated. The tabulæ often inosculate, and become to some extent vesicular, but these structures are comparatively few in number, and the "cystoid" character of the tabulæ is thus little marked. The genus *Pleurodictyum* is wholly Silurian and Devonian, so far as known, if *Michelinia* be excluded from it. The best known species is the *P. problematicum* of the Devonian rocks of Europe, the singular discoid casts of which (fig. 200, A) are commonly found in the Lower Devonian of the Eifel. In these casts the conical columns (fig. 200, B) represent the moulds of the visceral chambers of the corallites, and the little cylindrical rods connecting these are the result of the infilling of the mural pores. A singular feature in these casts is, that there is generally to be seen a curious cylindrical twisted body (fig. 200, A) in the centre of the base. This "worm-like body" has been very generally recognised in specimens of

Pleurodictyum, of different species and from widely remote regions. There is little reason to doubt that it represents the tube of an Annelide which lived as a "commensal" with the coral, in the same

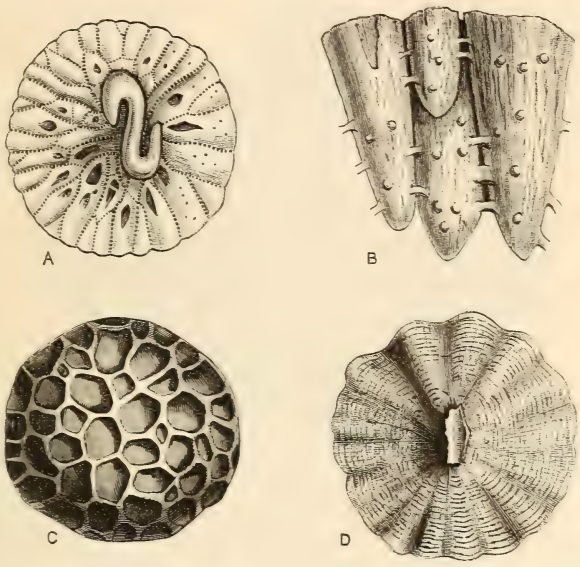


Fig 200.—A, Lower surface of the cast of *Pleurodictyum problematicum*, Goldf., from the Lower Devonian of Germany, of the natural size (after Roemer), showing the vermiform body in the centre; B, A few of the separate casts of the tubes of *Pleurodictyum problematicum*, Goldf., from the Devonian of the Eifel, showing the casts of the mural pores, enlarged (after Milne-Edwards and Haime); C, Upper surface of the corallum of *Pleurodictyum stylophorum*, Eaton, from the Hamilton group of North America, of the natural size, showing the form of the calices (Original); D, Lower surface of another example of the same, of the natural size, showing the striated epitheca, and the point where the corallum was attached to the stem of a Crinoid (Original).

way as a Sipunculid (*Aspidosiphon*) is found in constant association with the corallum of the existing *Heteropsammia*.

The genus *Michelinia* is in all its essential characters identical with *Pleurodictyum*, but the corallum is massive (fig. 201), and the tabulæ are numerous, and inosculate so as to give rise to a tissue of arched vesicles. The epitheca, also, commonly gives off root-like processes of attachment. The species of *Michelinia* are all Devonian and Carboniferous.

It remains to briefly notice certain transitional types by which the *Favositidæ* are connected with the *Poritidæ* on the one hand and the *Syringoporidæ* on the other hand. Thus, a near approach to *Alveopora* among the *Poritidæ* is effected by the remarkable Ordovician genus *Calapœcia* (=*Columnopora*).[1] The corallum in this genus is massive, and is com-

[1] An examination of the original specimens has clearly shown that the forms described by Billings under the name of *Calapœcia* are identical with those

posed of polygonal corallites, which are usually directly connected by their walls, and agree with those of the *Favositidæ* in possessing a primordial mural plate. A true cœnenchyma is in general wanting, but in some

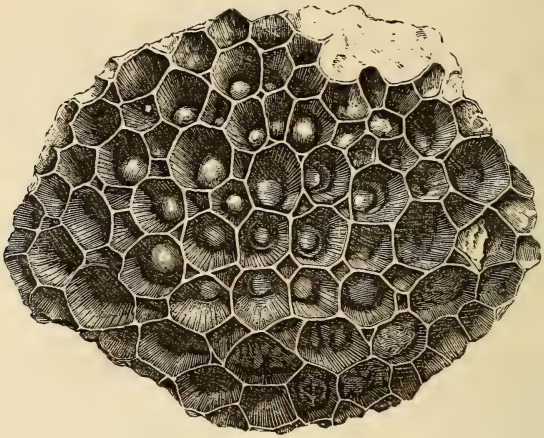


Fig. 201.—*Michelinia convexa* (D'Orbigny). Devonian.

specimens the corallites are in places connected by the intervention of a small quantity of exothecal tissue. The walls of the corallites are perforated by rows of large mural pores, which are placed close together and give the wall a lattice-like appearance. The septa are in the form of

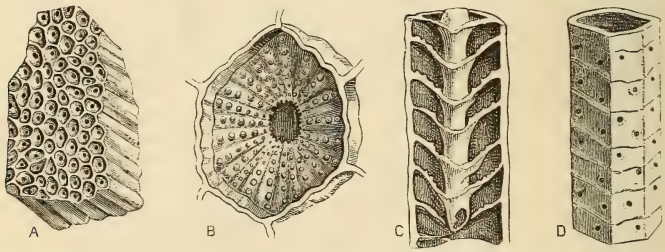


Fig. 202.—A, A fragment of a colony of *Syringolites Huronensis*, Hinde, of the natural size; B, A single calice of the same, enlarged eight times, showing the central tube, and radiating lines of septal tubercles; C, Part of a corallite of the same, split open, and enlarged six times, showing the composition of the central tube out of invaginated tabulæ; D, Part of a corallite of the same, viewed from the exterior and enlarged six times, showing the mural pores. Niagara Limestone, Manitoulin Island, Ontario. (Original.)

marginal ridges, and the tabulæ are complete and horizontal, and do not give rise to a vesicular tissue by their union.

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described by the present writer under the head of *Columnopora*, and the latter name must therefore be abandoned. Of the forms included by Billings under *Calapœcia*, only one—viz., *C. Anticostiensis*—was figured, and this proves to be really quite different from the others, and to be nearly related to the genera *Syringophyllum* and *Thecostegites*.

On the other hand, a distinct transition between *Favosites* and *Syringopora* is effected by the Silurian genus *Syringolites*, in which the corallum (fig. 202) is quite similar in general structure to *Favosites*, being composed of thin-walled polygonal corallites, the faces of which are perforated by longitudinal rows of distant mural pores, but the tabulæ are curved, and are depressed centrally so as to produce by their invagination a vertical median tube running down the middle of each visceral chamber. The Devonian genus *Roemeria*, again, seems to offer a similar transition between *Pachypora* and *Syringopora*. In this remarkable type, the corallum is closely similar in general structure to that of *Pachypora*, being composed of contiguous polygonal corallites, with distinct walls which are greatly thickened internally by a secondary deposit of stereoplasma, and are perforated by well-marked tubular mural pores, but the tabulæ are funnel-shaped and are invaginated in a manner precisely similar to that which is so characteristic of *Syringopora*.

The genus *Romingeria*, of the Silurian and Devonian rocks of North America, affords another transitional link between the *Favositidæ* and the *Syringoporidæ*. The corallum in this genus (fig. 203) is lax and spreading, erect or semi-erect, and composed of cylindrical tubular corallites which are produced by gemmation in umbellate whorls or verticils. The tubes are largely free, but where their walls come in contact, the visceral chambers are placed in communication by distinct mural pores. The tabulæ are remote, and in general horizontal, and the septa are represented by vertical rows of calcareous spines.

Fig. 203.—Portion of the corallum of *Romingeria umbellifera*, of the natural size. Devonian (Corniferous Limestone), Canada. (Original.)

Family 5. *Syringoporidæ*.—This family includes a number of Palæozoic corals in which the skeleton is composite, usually fasciculate in form (figs. 204-207), and is composed of cylindrical corallites which in general are not in actual contact, but mostly have their visceral chambers placed in direct communication by means of hollow, cylindrical connecting-processes or horizontal platforms, which are periodically produced. In many cases the corallites come into actual contact in parts of the corallum, and where this occurs their walls are pierced by mural pores similar to those of the *Favositidæ*. The tabulæ are well developed, and are usually funnel-shaped, but they are sometimes vesicular, or may, rarely, be simply curved. The septa are in the form of vertical rows of calcareous spines. The mode of increase is by basal or stolonal gemmation, or by the production of new buds from the connecting-processes or floors. The oldest members of this family appear in the Ordovician rocks, and the last appear in the Carboniferous.

The affinities of the *Syringoporidæ* have been much disputed, and the type-genus *Syringopora* has commonly been placed among the *Alcyonaria*, and has been regarded as a near ally of the recent

Tubipora. To the present writer the evidence in favour of the view that the *Syringoporidæ* constitute a peculiar group of the *Madreporaria Perforata*, and that they are nearly related to the *Favositidæ*, appears to be exceedingly strong, and may be briefly summed up as follows :—

a. The hollow connecting-processes of *Syringopora* are morphologically nothing more than mural pores as existing between corallites which are not in actual contact, and, like mural pores, they place the visceral chambers of contiguous tubes in direct communication.

b. In many members of the *Syringoporidæ* the corallites *do*

Fig. 204.—*Syringopora retiformis*. Silurian.

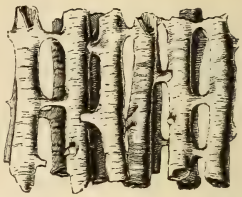

Fig. 205.—*Syringopora verticillata*. Silurian.

Fig. 206.—*Syringopora Dalmani*. Silurian.

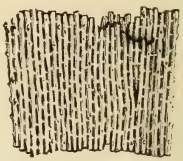

Fig. 207.—*Syringopora compacta*. Silurian.

partially come into direct contact, and wherever this occurs, mural pores of the ordinary Favositoid type are developed.

c. The septa have the form of vertical rows of calcareous spines, as is also the case in the typical members of the *Favositidæ*.

d. The Favositoid genera *Syringolites* and *Roemeria* possess the infundibuliform tabulæ of *Syringopora* in combination with the contiguous corallites and serially disposed mural pores of *Favosites* and *Pachypora*.

e. On the other hand, the Syringoporoid genera *Cannapora*, *Chonostegites*, *Thecostegites*, and *Syringophyllum* have the general characters of *Syringopora* as regards the form of the corallum and the mode of increase, but resemble different members of the *Favositidæ* in the characters of the tabulæ, and, occasionally, in the possession of "mural pores."

f. Lastly, the skeleton in *Syringopora* and its allies is never composed of spicules, as it is in *Tubipora*, but its microscopic structure agrees precisely with that of the corallum in the *Madreporaria* generally.

It should be added, however, that though it would appear highly probable that the real affinities of the *Syringoporidæ* are with the *Madreporaria*, the members of this family show a resemblance to the Alcyonarians in the fact that their common mode of increase is by stolonal or basal gemmation, and in this respect they differ altogether from the typical Perforate Madreporarians; though this single feature cannot be allowed to counterbalance their numerous and striking points of resemblance to the *Favositidæ*.

The typical genus of the *Syringoporidæ* is *Syringopora* itself, in which the corallum commences as a prostrate network of tubes, resembling in form a colony of *Aulopora*. In process of growth, this basal network sends up numerous vertical, flexuous, cylindrical corallites, which are not in direct contact, though sometimes (*e.g.*, in *S. laxata*) they become directly united here and there. The corallites are enclosed, each, in a thick proper wall, and they are usually united by hollow cylindrical connecting-processes (figs. 204-207) which occasionally (*e.g.*, in *S. tabulata*) assume the form of horizontal laminar floors. These connecting-processes place the visceral chambers of adjoining tubes in direct communication, and, as shown in thin sections (fig. 208), they are traversed by continuations of the endothecal tissue of the polypes themselves. The septa are sometimes nearly obsolete, but they usually have the form of vertical rows of calcareous spines. The tabulæ are well developed, and are in general more or less regularly funnel-shaped (fig. 208, A), and give rise by their invagination to a more or less continuous tube occupying the axis of the visceral chamber. The species of *Syringopora* are abundant in the Silurian, Devonian, and Carboniferous deposits, and often reach a large size.

In the Silurian genus *Cannapora*, the general form of the corallum is like that of *Syringopora*, but when connecting-processes are present these are very short, and the corallites are usually partially in contact, in which case they assume a polygonal form and are perforated by mural pores. The tabulæ are sometimes funnel-shaped, sometimes simply curved, and the septa are spiniform.

We may also include in this family the remarkable Devonian genus *Chonostegites*, which proves to be a link between the *Syringoporidæ* and *Favositidæ*, and has, indeed, been included in the latter family. The corallum in this genus is massive, and is composed of cylindrical corallites which may be partially in contact, but are usually separate and are connected by numerous close-set, concentrically disposed, horizontal connecting-floors or laminar expansions. These periodic floors are so far exothecal that they are extensions from the walls of the corallites, but they are hollow, and are filled with prolongations of the endothecal tissues of the corallites themselves, so that they place the visceral chambers of contiguous tubes in direct communication. In places, the corallites come into direct contact, and in this case their visceral chambers communicate by mural pores precisely similar to those of the *Favositidæ*. The septa have the form of rows of calcareous spines, and the tabulæ differ from those of *Syringopora* and

agree with those of *Michelinia* in being vesicular or "cystoid" in structure. The increase of the corallum is by basal gemmation, or by budding from the hollow periodic expansions in the intervals between the old cups. In the mode of increase, *Chonostegites* resembles *Syringopora*, and the hollow periodic floors may be considered as homologous with the hollow connecting-tubes of the latter. On the other hand, in the possession of vesicular tabulæ and in the presence of mural pores in parts where the corallites touch each other, the genus closely approaches to *Michelinia*. Nearly related to *Chonostegites* is the Ordovician and Silurian genus *Syringophyllum*, and we may also place here the Devonian genus *Thecostegites*. In both these genera the corallum consists essentially of cylindrical, tabulate corallites which are placed in connection with one another by hollow, periodically produced, laminar floors, into which the endothecal tissues of the polypes are directly continued; but in some cases these floors are successively superimposed on one another, and give rise by their union to a kind of spurious cœnenchyma. The structure of the skeleton in these genera is, however, too complex to allow of its being advantageously considered here.

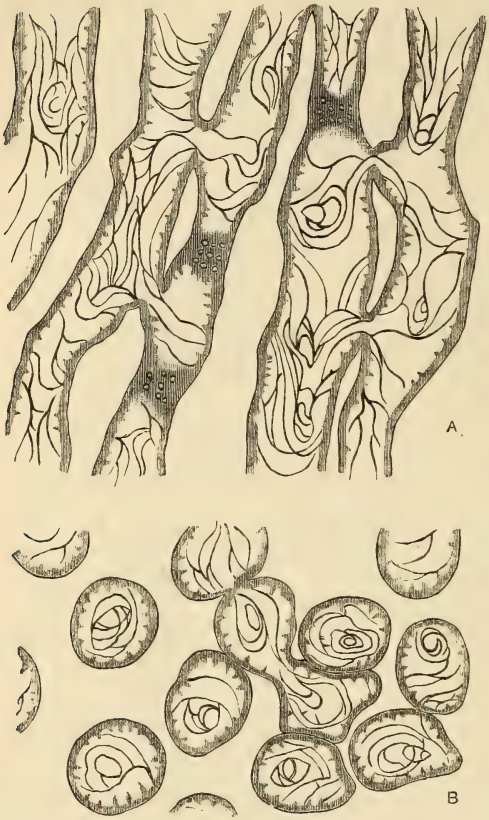

Fig. 208.—A, Part of a longitudinal section of *Syringopora reticulata*, Goldf., from the Carboniferous Limestone of Kendal, Westmorland, enlarged five times, showing the spiniform septa and the funnel-shaped tabulæ with their central tube. Owing to the flexures of the corallites, the section cuts the tubes in different parts, sometimes passing close to the wall and showing the cut ends of the spiniform septa, sometimes passing through the axis of the visceral chamber and bisecting the axial tube, and sometimes cutting the axial tube and its enveloping tabulæ in an oblique manner. B, Part of a transverse section of the same specimen, enlarged five times, showing the spiniform septa, and the cut edges of the tabulæ surrounding the central tube. (Original.)

Family 6. *Thecidæ*.—This family includes only the aberrant genus *Thecia*,[1] the structure of which is too complex to permit of more than

[1] As the result of extended investigations, the writer has been led to materially modify the views which he formerly expressed ('Palæozoic Tabulate Corals') as

the briefest description in this place. The corallum in *Thecia* is generally in the form of a laminar expansion, furnished inferiorly with a striated epithecal membrane. In their early condition, the corallites are often oblique to the basal plate, and in this stage they have thin and apparently distinct walls, the visceral chambers being crossed by complete tabulæ, and the general appearance being not unlike to that of some species of *Favosites*. Very soon, however, the corallites become perpendicular to the basal plate, and they then appear to lose their distinct walls and to become united by the intervention of a thick, vertically tubulated calcareous tissue, which may be regarded as probably of the nature of a spurious cœnenchyma, and from which the walls of the individual corallites are wholly inseparable. The surface, therefore, exhibits the stellate calices of the corallites separated by an apparently dense interstitial tissue, marked superficially by minute tubercles, and by radiating, often vermicular, grooves which extend from one calice to another. The visceral chambers of adjacent corallites are placed in direct communication by means of well-marked, often bent, horizontal tubes, which represent elongated mural pores. The septa are generally twelve in number in each corallite, and have the form of irregular vertical ridges, with very broad bases, which only extend a short way inwards into the visceral chamber, and appear sometimes to terminate along their inner edges in blunt spines. The tabulæ are complete, horizontal, or slightly curved, and tolerably numerous.

The known species of *Thecia* are Silurian, the most familiar being the common *T. Swindernana* of the Wenlock Limestone. The coral described by Rominger from the corresponding horizon in America under the name of *Thecia major* appears to differ in important respects from the European species of *Thecia*, and would appear to be nearly related to the Favositoid genus *Laceripora*.

The family of the *Thecidæ*, as above defined, is separated from the *Favositidæ* by the complete fusion of the corallites in the terminal portion of their course, and by the peculiar nature of the tubulated cœnenchymal tissue which separates adjoining visceral chambers. The fact that the corallites have as a rule twelve septa each, would support the view that *Thecia* is to be regarded as referable to the *Zoantharia* rather than to the *Alcyonaria;* and the presence of tubes directly connecting the cavities of adjoining polypes would show that the genus belongs to the *Madreporaria Perforata*.

to the structure and affinities of *Thecia*. The exothecal tubules were previously regarded as corresponding with the "mesopores" of *Heliolites*, and the genus was on this ground placed among the *Alcyonaria*. The examination of well-preserved specimens by means of thin sections would, however, appear to prove conclusively that this is not their nature, and that they are really what Milne-Edwards and Haime described as a "spurious cœnenchyma."

CHAPTER XX.

GENERAL CHARACTERS AND DIVISIONS OF THE ALCYONARIA.

THE second great division of the *Actinozoa* is that of the *Alcyonaria* or *Octactiniæ*, defined by the possession of *polypes with eight pinnately fringed tentacles, the mesenteries and intermesenteric chambers being also eight in number. The corallum is usually sclerobasic, or spicular, or formed of both an axial sclerobasis and detached spicules. In other types, the polypes composing the colony may be provided with separate "thecæ."*

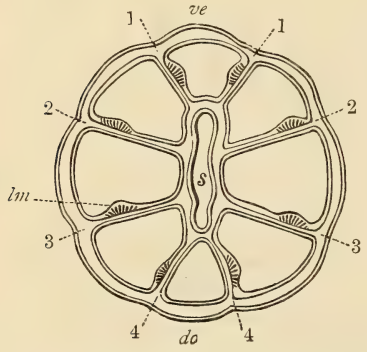

Fig. 209.—Transverse section of a polype of *Alcyonium*, enlarged. (After O. and R. Hertwig.) The numbers indicate the four pairs of mesenteries. *s*, Œsophagus transversely divided; *lm*, One of the eight longitudinal "retractor" muscles of the mesenteries; *ve*, Ventral side of polype; *do*, Dorsal side. Nos. 1 1, and 4 4, are the "directive" mesenteries.

The *Alcyonaria* are essentially distinguished from the *Zoantharia* by the possession of eight unpaired mesenteries and eight tentacles (reduced in some rare cases to six or four).

The mesenteries (fig. 209) are symmetrically grouped round the œsophagus, so that there is a dorsal intermesenteric space, and a ventral one, together with three lateral compartments on each side. The "directive" mesenteries of the ventral side (fig. 209, Nos. 1, 1), have the longitudinal retractor muscles attached to their opposed faces; whilst the opposed sides of the dorsal directive mesenteries have the transverse muscles. The mesenteries are not in pairs; and the order in which they appear has not been precisely investigated, the numbering given in the annexed figure not being certainly known to express the order in which these structures are developed.

With the exception of the two genera *Monoxenia* (*Haimeia*, E. and H.) and *Hartea*, the *Alcyonaria* are all composite, the tubular polypes being united by a cœnosarc, and their body-cavities being placed in communication by means of anastomosing canals, which ramify in the cœnosarc, and permit of a free circulation of nutrient fluids. The form of the colony differs greatly in different cases, but none possess the power of independent locomotion, most being rooted to foreign objects, or sunk in the mud. The polypes, in most of the essential points of their organisation, agree with those of the *Zoantharia*, the mouth opening into a tubular gullet, which in turn communicates freely with the body-cavity, and the œsophagus being connected with the body-wall by means of a series of vertical membranous laminæ or "mesenteries." The mesenteries, however, are only eight in number, and are not paired, one of the tentacles corresponding with and opening into each intermesenteric chamber.

The gullet in the *Alcyonaria* is so placed that its long axis (fig. 209) corresponds with the dorso-ventral plane of the body of the polype, and it very commonly is furnished on its ventral side with a ciliated groove (the "siphonoglyphe" of Mr Hickson).

In many instances the colony in the *Alcyonaria* is dimorphic, consisting of two sets of zoöids, which differ from one another in structure and function. The zoöids of the one series (generally called "autozoöids) have the normal size, and possess the structures proper to the mature polypes; while those of the other series (generally called "siphonozoöids") are reduced in size, and want certain structures of the normal polypes, such as tentacles, mesenterial filaments, or reproductive organs. No siphonozoöids have been recognised in *Tubipora* or in most of the *Gorgonidæ*, and von Koch doubts if the structures described as such by Moseley in *Heliopora* are really of this nature.

The mode of increase in the *Alcyonaria* is typically by basal or stolonal gemmation, the parent throwing out basal extensions, which commonly unite to form a creeping network or a crust-like expansion, from which new polypes are thrown up at intervals. In other cases the stolons are produced from the sides of the polypes at different levels above the base; and in still other cases (*e.g.*, in *Alcyonium*) the stolons coalesce to form a common fleshy mass or cœnosarc. In some cases, as in the *Heliolitidæ*, the peculiar mode of increase which has been described by von Koch as "cœnenchymal gemmation" is observed, but the nature of this will be described hereafter.

There are no skeletal structures in *Monoxenia* (*Haimeia*), but with this exception a corallum of some sort or another is produced in all the *Alcyonaria*. According to the investigations of von Koch, the skeletal structures of the *Alcyonaria* may be ectodermal or mesodermal in origin. The ectoderm commonly produces hard struc-

tures of a horny character, in general hardened by the deposition of carbonate of lime. In some cases (*e.g.*, in *Cornularia*) these horny structures remain external, forming a sheath to the colony; but in other cases the colony becomes in process of growth inverted over the skeleton, which then forms a central horny axis or "sclerobase" supporting the soft parts (fig. 210). The mesoderm may also produce skeletal structures in the form of variously-shaped crystalline spicules or "sclerites" (fig. 123), which are composed of an organic basis hardened by carbonate of lime. In some Alcyonarians the skeleton consists solely of these mesodermal spicules, which may remain entirely free and detached (as in *Alcyonium*), or may be fused with one another directly (as in *Corallium* and *Tubipora*), or may be partly free and partly united by horny matter (as in *Sclerogorgia*). In other types, again, as in *Gorgonia* and *Isis*, the skeleton is twofold, consisting on the one hand of an axial sclerobase of ectodermal origin, and on the other hand of free spicules developed within the mesoderm. The skeleton of *Heliopora*, finally, is peculiar in its structure, and is probably ectodermal in origin.

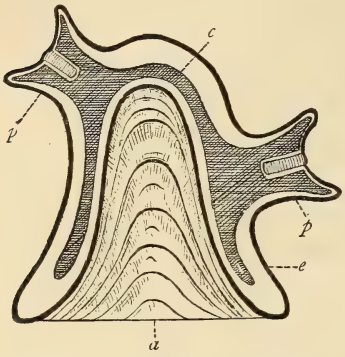

Fig. 210.—Diagrammatic vertical section through a young colony of *Gorgonia*, showing the relation of the sclerobase to the soft parts. *a*, Horny axis or sclerobase, supporting the colony; *e*, Ectoderm represented by the thick dark line; *p p*, Two polypes; *c*, One of the cœnosarcal canals, connecting the visceral chambers of the polypes with one another. For the sake of clearness, the horny axis has been represented of disproportionate thickness. (After von Koch.)

The *Alcyonaria*, so far as the living types are concerned, are divided by von Koch into the following groups:—

SUB-ORDER I. ALCYONACEA.—Sedentary Alcyonarians in which an axial skeleton is usually wanting. When such a skeleton exists (as in *Corallium*) it is of mesodermal origin, and is not secreted by a continuous epithelial layer.

Family 1.	Haimeidæ, . . .	*Monoxenia, Hartea.*
" 2.	Cornularidæ, . .	*Cornularia, &c.*
" 3.	Alcyonidæ, . . .	*Alcyonium, &c.*
" 4.	Pseudaxonia, . .	*Corallium, Mopsea, &c.*
" 5.	Tubiporidæ, . . .	*Tubipora.*
" 6.	Helioporidæ, . . .	*Heliopora.*

SUB-ORDER II. GORGONACEA.—Sedentary Alcyonarians in which there is a firm sclerobasic axis secreted by a continuous epithelial layer. The colony is not polymorphic.

Family 7.	Gorgonidæ, . . .	*Gorgonia, Isis, &c.*

Sub-order III. Pennatulacea.—Free-living Alcyonarians consisting of a stem and polypiferous branches. The colony is polymorphic.

Family 8. Pennatulidæ, . . . *Pennatula*, *Veretillum*, &c.

So far as the sub-orders are concerned, the above classification is only partially available for palæontological purposes, as based upon characters which are not recognisable in fossil forms. There are, moreover, certain extinct groups of corals (*Halysitidæ*, *Tetradiidæ*, *Chætetidæ*, &c.) which we must provisionally place among the Alcyonarians, but which cannot, with our present knowledge, be included in any of the three sub-orders above mentioned.

As regards the *distribution in time* of the Alcyonarians, the families of the *Haimeidæ*, *Cornularidæ*, *Alcyonidæ*, and *Tubiporidæ* have no fossil representatives, so far as is certainly known; and only the last mentioned of these requires further notice here. On the other hand, the families of the *Pseudaxonia*, *Gorgonidæ*, *Pennatulidæ*, and *Helioporidæ* are all sparingly represented by fossil types in the Secondary and Tertiary deposits. The extinct family of the *Heliolitidæ* is mainly Palæozoic, its earliest representatives appearing in the Ordovician rocks. In addition to the preceding, there are the four families of the *Halysitidæ*, *Tetradiidæ*, *Chætetidæ*, and *Auloporidæ*, the members of which are apparently exclusively Palæozoic, but the true relationships of which are more or less uncertain. Still more uncertain is the systematic position of the extinct groups of the *Monticuliporidæ* and *Fistuliporidæ*, which will be here treated of apart from the *Alcyonaria*.

In the following brief account of the fossil Alcyonarians, only those families will be considered which are known to have fossil representatives; but the family of the *Tubiporidæ* also demands a short notice, from its supposed relationship to *Syringopora*.

Pseudaxonia.

This group of the Alcyonarians comprises forms in which the skeleton is composed of mesodermal spicules, the sclerobasic axis, when present, not being secreted by a continuous epithelial layer. The spicules are sometimes (*Briareum*) completely detached, though even in this case they may form in part a tolerably well-defined axis. On the other hand, in the well-known Red Coral (*Corallium rubrum*) there is a dense calcareous sclerobase which is composed of spicules or sclerites embedded in and united by a fibro-crystalline calcareous matrix (fig. 211). The sclerobasic axis of *Corallium* is unjointed and is branched, and its surface exhibits longitudinal grooves which lodged the larger cœnosarcal canals (fig. 124). In *Melithæa* and *Mopsea*, again, there is a sclerobasic axis, but this is jointed, and is com-

posed alternately of soft and hard segments, the former being composed of separate sclerites united by horny matter, while the latter are made up of fused spicules. In *Sclerogorgia*, finally, there is an unjointed axis, consisting of horn with embedded sclerites, while there are also free spicules in the soft tissues.

As regards the geological distribution of the *Pseudaxonia*, the genus *Corallium* appears to be represented in rocks as ancient as

Fig. 211.—Part of a longitudinal section of *Corallium rubrum*, magnified 180 times, showing the spicules of the skeleton united by a crystalline or fibrous matrix, produced by the calcification of the soft interspicular tissues. (Original.)

the Jurassic, and the Eocene Tertiary has yielded the remains of the genera *Mopsea* and *Websteria*, of which the former still survives, while the latter is confined to the Eocene and is of uncertain affinities.

Tubiporidæ.

This group of the Alcyonarians comprises only the recent genus *Tubipora*, including the familiar "Organ-pipe Corals." There is a well-developed corallum in *Tubipora* composed of numerous cylindrical tubes or thecæ, separated by small intervals, and connected with one another by horizontal calcareous floors, which form a series of concentric laminæ parallel with the upper surface of the colony. These floors are produced by the coalescence of horizontal stolons given out from the upper ends of the polypes, and new corallites are budded out from their upper surface. Internally they are traversed by horizontal canals which communicate with the visceral chambers

of the polypes by numerous rounded apertures placed at the points where the corallites are embraced by the floors (fig. 212, A and B).

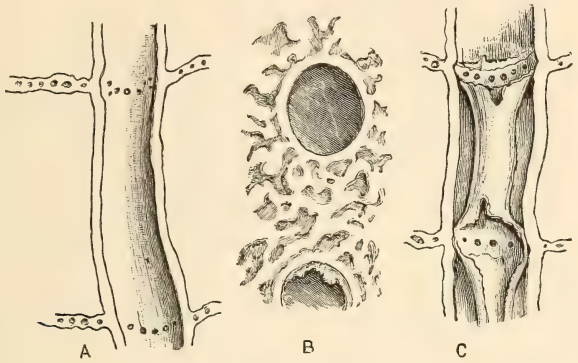

Fig. 212.—A, Part of a tube of *Tubipora musica*, Linn., divided longitudinally, showing the openings of the canal-system of the connecting-floors into the visceral chamber of the polype; B, Part of a horizontal section taken at the level of one of the connecting-floors, showing the canal-system of the connecting-floor; C, Part of a corallite of *Tubipora* divided longitudinally, showing the axial tube; in the lower portion of the figure the axial tube is laid open. All the figures are enlarged five times. (Original.)

In the interior of the corallites there commonly exists a hollow calcareous tube (fig. 212, C), which occupies the axis of the visceral

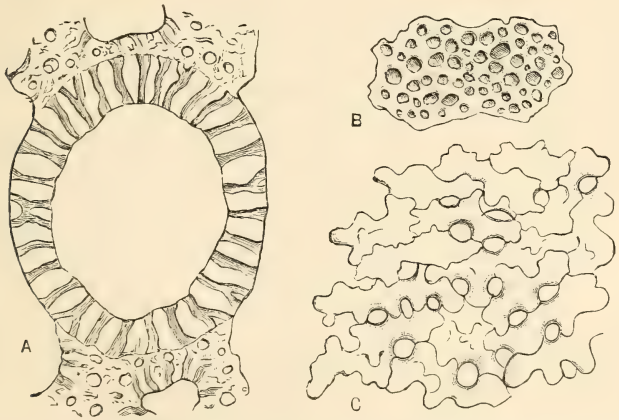

Fig. 213.—A, Transverse section of a corallite of *Tubipora musica*, Linn., taken at the level of one of the connecting-floors, enlarged twenty times, showing the tubuli of the wall; B, Portion of the surface of one of the connecting-floors, enlarged twenty times, showing the external openings of the tubuli of the skeleton; C, Fragment of the corallum of *Tubipora*, enlarged sixty times, showing the composition of the skeleton out of spicules. (Original.)

chamber, and is dilated and fused with the enclosing theca at the level of the successive connecting-floors. This axial tube is only

occasionally present; and no traces of proper "tabulæ" (in the strict sense) have been noticed to occur. There are also no structures which admit of being regarded as septa.

As regards the microscopic structure of the corallum of *Tubipora*, the entire calcareous skeleton is permeated throughout by a system of minute parallel tubules, which sometimes branch, and which open on the surface by well-defined rounded apertures (fig. 213, A and B). These canaliculi run at right angles to the walls of the corallites and also to the connecting-floors, and they render the skeleton of *Tubipora* completely and minutely porous. Moreover, thin sections show that the skeleton is made up of a network of irregular fusiform spicules which are firmly united with one another (fig. 213, C).

The genus *Tubipora* is not known to occur in a fossil condition, but the structure of its skeleton is a matter of considerable palæontological importance, as high authorities regard the genus as the closest living ally of the Palæozoic genus *Syringopora*. Reasons have been previously given (p. 320) for considering that *Syringopora* and its allies are closely related to the *Favositidæ*, and that they truly form a group of the *Madreporaria Perforata*. It is sufficient, therefore, to point out here that the skeleton of *Tubipora* differs fundamentally from that of *Syringopora* in the following points:—

a. The entire skeleton is traversed by minute canaliculi, no traces of which are found in the compact corallum of *Syringopora*.

b. The skeleton is composed of distinct spicules.

c. The axial tube, when present, is not formed of invaginated "tabulæ," as in *Syringopora*, and there is no evidence of the existence of proper "tabulæ" at all.

d. No proper septa exist, whereas well-developed spiniform septa are present in *Syringopora*.

Upon the whole, therefore, it would appear that there is no sufficient evidence at present available which would support the reference of *Syringopora* and its allies to the *Tubiporidæ*.

Gorgonidæ.

The family of the *Gorgonidæ*, as defined by von Koch, includes those Alcyonarians in which the colony is fixed, and is supported by an axial sclerobase, which is secreted by a continuous layer of epithelium. The sclerobase may be purely horny (as in *Gorgonia* itself), or it may be composed of alternate horny and calcareous joints (as in *Isis*). The polypes are all similar to one another, and polymorphism has not been observed. This family is of little palæontological importance; but the genus *Isis* has been recognised in deposits as ancient as the Cretaceous. Remains re-

ferable to the recent genera *Primnoa* and *Gorgonella* have also been detected in the Miocene Tertiary rocks.

Pennatulidæ.

This family includes a number of Alcyonarians in which the colony is not fixed to any foreign object, and is composed of a central cœnosarcal stem or rachis carrying polypes superiorly, these being commonly arranged on longer or shorter lateral branches. The polypes are dimorphic, and the skeleton usually has the form of an unbranched, horny or partially calcified sclerobase. This group is also of small palæontological importance, but the genus *Pavonaria* has been recognised in deposits of late Cretaceous age, and the remains of *Graphularia* have been found in the Eocene and Miocene Tertiary.

Helioporidæ.

This family, as here defined, comprises only the single genus *Heliopora*, in which there is a well-developed sclerodermic corallum (fig. 214, A) composed of tabulate tubes of two sizes, the larger of these being furnished with radiating pseudosepta, which do not correspond in number with the mesenteries of the living polypes. The larger tubes of the colony ("autopores") have usually been regarded as the true corallites, and the smaller interstitial tubes ("siphonopores") have been commonly considered as constituting a "cœnenchyma"; but the researches of Moseley on the living *Heliopora cærulea* have rendered it probable that the colony is really dimorphic, the sexual zoöids occupying the large tubes, while the small tubes lodge imperfect sexless zoöids. The large tubes or "autopores" are crossed by well-developed horizontal "tabulæ," and are completely separated from one another by the smaller tubes or "siphonopores," which are also tabulate (fig. 214, C). Apart from their larger size, the autopores are further distinguished by the fact that they exhibit internally a variable number of longitudinal ridges which resemble the radiating "septa" of the Zoantharian corals. In the living *Heliopora cærulea* there are usually twelve of these radiating ridges in each autopore, but they can hardly be said to have any existence as definite structures, and appear rather to be formed by the projection into the cavity of the autopore of the prismatic siphonopores which bound the latter. In *H. Partschii*, of the Cretaceous rocks, the autopores possess from twenty-five to twenty-eight radial ridges which extend inwards to some distance, while *H. macrostoma*, of the same formation, has numerous septal ridges, but these are shorter. In any case these septal ridges not

only are not at all constant in number, but do not correspond with the mesenteries of the living polypes, these being always *eight* in number. Hence, the radial ridges of *Heliopora* must be regarded as "pseudosepta," and they are not homologous with the "septa" of the Madreporarians. The "siphonopores" or interstitial tubes are destitute of pseudosepta, and in the case of the living *H. cærulea* they are occupied by structures which Professor Moseley regards as

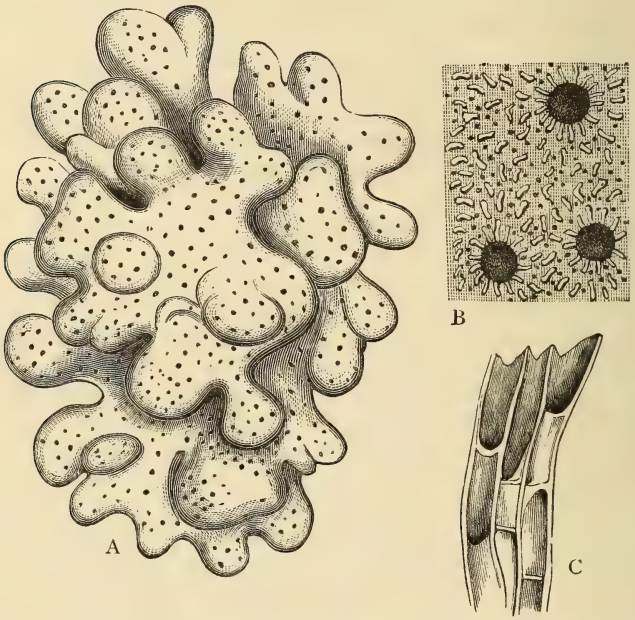

Fig. 214.—A, Colony of the recent *Heliopora cærulea*, of the natural size; B, Portion of the surface of the same, enlarged, showing the apertures of the larger and smaller zoöids; C, Vertical section of a few of the "siphonopores" enlarged, showing the tabulæ. (After Dana.)

probably of the nature of rudimentary, sexless polypes. These "siphonozoöids" have the form of sacs lined by the endoderm, closed externally, but communicating with the cavities of the autozoöids by means of canals in the soft tissues.

As regards its minute structure, the skeleton of *Heliopora* consists of fibro-crystalline carbonate of lime having a very peculiar and characteristic arrangement. When examined in thin sections (fig. 215), the corallum is seen to be composed of radially disposed, parallel, prismatic rods, the apices of which project above the general surface as prominent blunt papillæ which occupy the angles of junction of contiguous siphonopores, and constitute a diagnostic feature of

the genus *Heliopora*. The rods are generally placed, each, at the junction of four siphonopores, and are, therefore, essentially quadrilateral. They are firmly united with one another along their opposed sides by dentated sutures, and they are excavated along their angles by the siphonopores. Each rod possesses a single or multiple, generally elongated, apparently structureless axis, round which the calcareous tissue is disposed in radiating plates of great tenuity, which look in cross-sections (fig. 215, A) like fibres. The peculiar prismatic rods just described may be regarded as modified spicules, which become laterally anchylosed. In the fossil species of

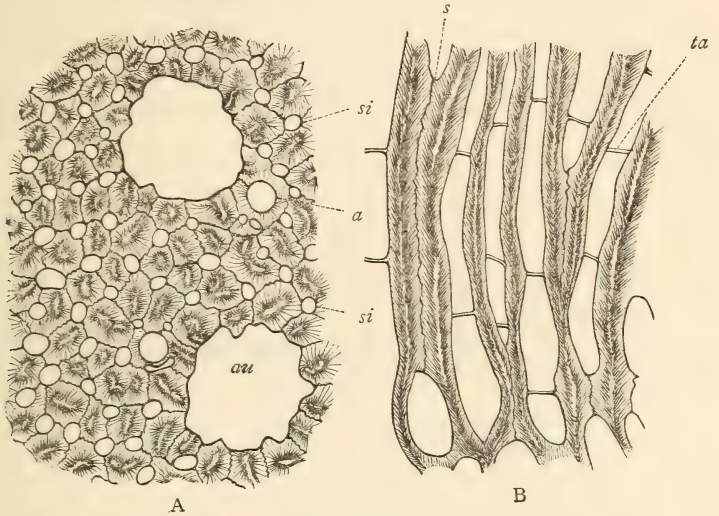

Fig 215.—A, Tangential section of the corallum of the recent *Heliopora cærulea*, enlarged twenty times; B, Longitudinal section, similarly enlarged. *au*, Autopore; *si*, Siphonopore; *a*, Tube of a parasitic Annelide (*Leucodora*); *s*, Suture between two adjoining spicules; *ta*, Tabula. (Original.)

Heliopora the skeletal structure is commonly largely affected by mineralisation, but in some cases (*e.g.*, in *H. Blainvilleana*) the minute structure of the corallum can be shown to be essentially similar to that of the recent *H. cærulea*. Even where obliterated by crystallisation, the minute structure can be inferred to have been spicular, as the surface always shows the characteristic projecting papillæ formed by the free ends of the skeletal rods.

It is worth noting in connection with the skeleton of *Heliopora* that the corallum in the recent *H. cærulea* is commonly traversed by numerous Annelide-tubes belonging to a species of *Leucodora*. These tubes are intermediate in size between the autopores and siphonopores (fig. 215, A), are very regularly distributed, and have their mouths flush with the general surface; while they are not mere borings, but are coated by

a layer of the coral-substance. For these reasons they have all the aspect of belonging to the corallum itself, and if they occurred in the fossil species of the genus their real nature might very readily be mistaken.

The mode of growth of the corallum in *Heliopora* is peculiar. The siphonopores appear to increase by means of "intermural gemmation," and not, as in the *Heliolitidæ* generally, by fission. On the other hand, the autopores, as can readily be observed in the growing ends of the colony, are produced by what von Koch has called "cœnenchymal gemmation." In this process—which will be spoken of again in connection with *Heliolites*—new autopores are produced by the apparent fusion and coalescence of a number of the siphonopores. According to Moseley's observations on the recent *H. cærulea*, this is effected by an arrest of growth of one or more of a group of siphonopores set apart for the production of a fresh autopore. "The arrested cell or cells form a central floor to the new calicle, around which lies a circular zone of contiguous, deeper, and older cells. The inner walls of these cells—*i.e.*, those nearer to the centre of the growing calicle—cease to grow, whilst their outer ones continue to develop, and being fused together form the lateral walls of the calicle. The plications in the wall of the fully formed calicle are to a great extent the result of this peculiar mode of growth." The conversion of a group of imperfect polypes into a single complete polype is doubtless a sufficiently remarkable phenomenon; but it is probable that, in reality, it is only a single siphonozoöid which ultimately becomes developed into an autozoöid, the remainder of the siphonozoöids concerned in the process becoming aborted. An analogous phenomenon has been observed by von Koch ('Zoologischer Anzeiger,' 1881) in the case of certain of the *Pennatulidæ*, in which the siphonozoöids become converted into autozoöids. The subject is one of great palæontological importance, since the same phenomenon—as will be subsequently shown—is observed in *Heliolites* and its allies; and it has been contended by Lindström that this fact is seriously opposed to the view that the interstitial tubes of *Heliolites* are of the nature of "siphonopores" rather than of "cœnenchymal tubes." The observations of Moseley upon *Heliopora cærulea* and of von Koch on the *Pennatulidæ* deprive this contention, however, of the weight which might otherwise be attached to it.

Since the researches of Moseley upon *Heliopora cærulea*, it has been usual to include *Heliolites* and its allies in the family of the *Helioporidæ*. The latter, however, possess a skeleton widely different from that of *Heliopora* in its minute structure, while the autopores are provided with an approximately constant number of septa, the nature of which appears to be different from that of the pseudo-

septa of *Heliopora*. For these reasons, amongst others, *Heliolites* and its relations may be placed, provisionally at any rate, in a separate family.

The recent *Heliopora cærulea* is found in the Indian and Pacific oceans, and fossil species of the genus are found in the Cretaceous and Eocene deposits. The imperfectly known genus *Polytremacis*, from the Cretaceous rocks, appears to be closely related to *Heliopora*.

HELIOLITIDÆ.

This family comprises a number of Palæozoic corals, of which the type is the widely distributed and abundant genus *Heliolites* itself, and is closely similar to the preceding group in its general characters. The corallum (fig. 216) is composite, and consists of two sets of tubes, of different sizes, of which the larger ("auto-

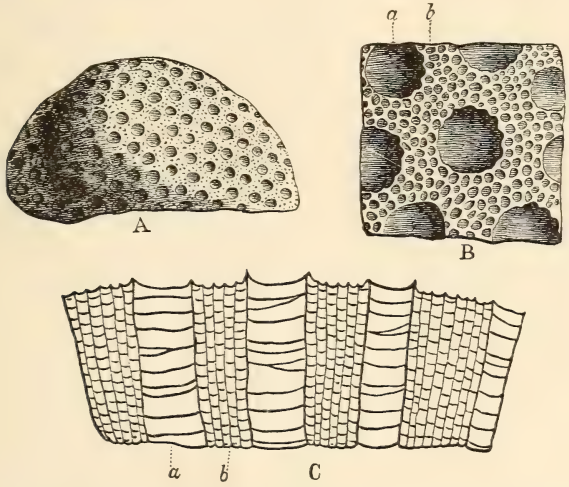

Fig. 216.—A, Small colony of *Heliolites interstinctus*, Linn., of the natural size; B, Small portion of the surface of the same, magnified, showing the autopores (*a*) and the mouths of the siphonopores (*b*); C, Vertical section of the same, enlarged, showing the tabulate autopores (*a*), and the similarly tabulate siphonopores (*b*). (Original.)

pores") are, as a rule, completely separated from one another by the intervention of the smaller ("siphonopores"). Both sets of tubes are provided with tabulæ (fig. 216, C), and the autopores are furnished with lamellar, or rarely spiniform, septa, the number of which is almost invariably twelve in each corallite. In some cases the septa unite centrally to form a reticulate pseudocolumella. The siphonopores increase principally by fission, though partly by intermural gemmation, while the autopores are produced by

"cœnenchymal gemmation." The structure of the skeleton is not spicular.

As regards the minute characters of the skeleton, the autopores and siphonopores are *thin-walled*, and no traces of the peculiar prismatic rods of the corallum of *Heliopora* can be detected. The siphonopores are generally so largely developed as to form a complete zone, of one or more rows, of small tubes between adjacent autopores (fig. 216, B); but in *Heliolites dubius* (fig. 217, A) the number of the siphonopores is much reduced, and contiguous autopores are largely in contact. Both sets of tubes are furnished with

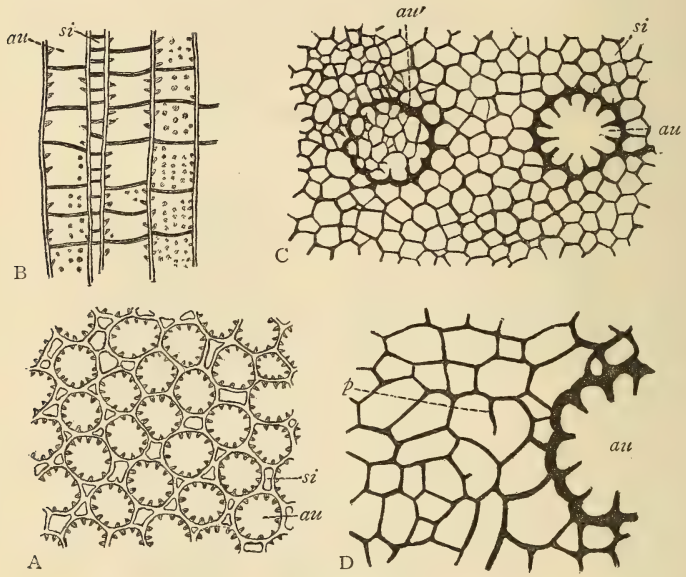

Fig. 217.—A, Cross-section of *Heliolites dubius*, from the Ordovician rocks of Esthonia, enlarged ten times; B, Vertical section of the same, similarly enlarged, showing the spiniform septa; C, Tangential section of *Heliolites porosus*, from the Middle Devonian of Büchel, showing "cœnenchymal gemmation," enlarged ten times; D, Part of another cross-section of the same, enlarged about twenty times, showing fission of the siphonopores. *si*, Siphonopores; *au*, Autopores; *au'*, Autopore being developed by "cœnenchymal gemmation"; *p*, Incomplete septum in a siphonopore, indicating partially accomplished fission of the tube. (Original.)

tabulæ, which are more numerous in the siphonopores than in the autopores (fig. 216, C). The siphonopores are without septa, but the autopores possess septal ridges or spines, which are very variable in their development, but are almost always twelve in number in each autopore. In some species (*Heliolites interstinctus*, *H. Murchisoni*, &c.) the septa are lamellar, but are rudimentary, and may even be represented only by slight bendings of the walls of the autopores. In other species (*H. porosus*, *H. parvistella*, &c.) the septa

are lamellar, and extend to a considerable distance into the interior of the visceral chamber, sometimes meeting to form a reticulated pseudocolumella (*H. intricatus*), or even showing alternate large and small septa (as in some examples of *Heliolites porosus*). Lastly, the septa may be in the form of twelve longitudinal rows of spines (as in *Heliolites dubius*, fig. 217, A and B, and in the true *Heliolites megastoma* of M'Coy).

As regards the mode of growth of the corallum in *Heliolites* and its allies, the siphonopores are usually developed fissiparously (fig. 217, D), though intermural gemmation also occurs. On the other hand, the autopores are produced by "cœnenchymal gemmation," in a fashion essentially similar to that which has been already described as occurring in *Heliopora*. In *Heliolites dubius*, in which the siphonopores are reduced to a minimum (fig. 217, A and B), a single siphonopore may sometimes be observed to be developed vertically and directly into an autopore. More usually, an autopore is produced by the arrested development of a group of siphonopores (as in *Heliopora*); and the process can be observed readily both in transverse and longitudinal sections. In the former (fig. 217, C) the enclosure of a group of siphonopores within an external wall, and the gradual development of the septa can be readily made out; while in long sections a few of the siphonopores are seen to be suddenly arrested in their growth, and commonly to be cut off by a common tabula, their place vertically being taken by a single autopore.

As regards their zoological position, the *Heliolitidæ* show points of relationship on the one hand to the *Alcyonaria*, and on the other hand to the *Zoantharia*. In the general features of the corallum (apart from the minute structure of the skeleton) the members of this family show a striking resemblance to the unquestionably Alcyonarian genus *Heliopora*, and in both groups we find the singular phenomenon of "cœnenchymal gemmation." This remarkable mode of increase, however, occurs also in the family of the *Fistuliporidæ;* so that undue weight must not be assigned to this alone. On the other hand, in the fact that the number of the septa is almost constantly twelve, while these structures are sometimes alternately long and short, and are occasionally in the form of rows of spines, we have a decided approach to various groups of the *Zoantharia*. The small tubes of the corallum of the *Heliolitidæ* have commonly been regarded as *cœnenchymal* in their nature, but Moseley's observations on *Heliopora* would strongly support the view here taken, that these structures are really tenanted by rudimentary polypes ("siphonozoöids"), and that the corallum is therefore really dimorphic. It has been already pointed out that the fact that the large corallites are formed by an arrested development and appa-

rent coalescence of a number of the small tubes does not really militate against the view that the latter are of the nature of "siphonopores."

As regards their *distribution in time*, all the members of the *Heliolitidæ* are Palæozoic, and all are confined to the Ordovician, Silurian, and Devonian periods.

The type-genus of the *Heliolitidæ* is *Heliolites* itself, in which the corallum is massive or branched, and the siphonopores are polygonal, and usually regular in form, and possess complete walls (figs. 216, 217). The species of *Heliolites* range from the Ordovician to the Devonian, and are very abundant in the Silurian rocks proper.

In the genus *Plasmopora* (fig. 218) the corallum is like that of *Heliolites* in general structure and appearance, but the walls of the

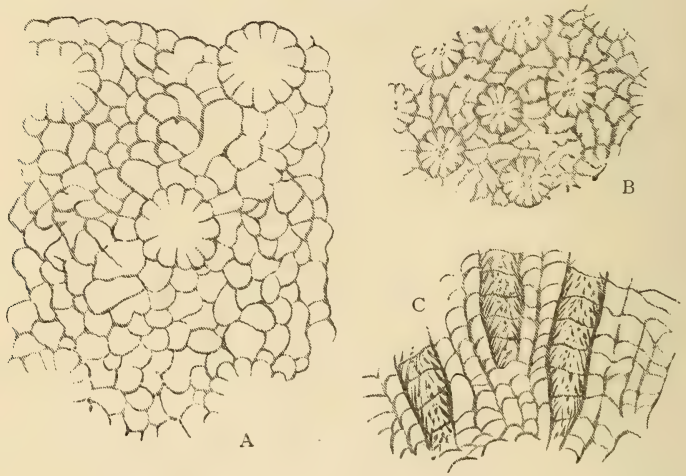

Fig. 218.—A, Transverse section of a specimen of *Plasmopora petaliformis*, Lonsd., from the Wenlock Limestone of Gotland, enlarged five times; B, Transverse section of *Plasmopora scita*, E. and H., from the Wenlock Limestone of Gotland, enlarged five times; C, Vertical section of the same specimen, similarly enlarged. (Original.)

siphonopores are incomplete or obsolete, and their tabulæ are thus enabled more or less largely to coalesce, and give rise to a vesicular tissue of lenticular cells (fig. 218). There are generally from two to five rows of siphonopores between adjoining autopores, and the septa may be either lamellar or spinulose. The species of *Plasmopora* are principally found in the Ordovician and Silurian rocks, but Devonian forms are also known. The Silurian deposits also contain various corals closely related to *Plasmopora*, for which the names of *Propora* and *Pinacopora* have been proposed, but these titles cannot be considered as of more than sub-generic value. In both these groups the siphonopores are much reduced in number, and the autopores are correspondingly close-set; the calices of the autopores being elevated above the general surface in *Propora*, but flush with the surface in *Pinacopora*, and the corallum in the latter being typically discoid in form.

HALYSITIDÆ.

This family comprises only the familiar Ordovician and Silurian corals known commonly as "Chain-corals," and constituting the single genus *Halysites*. The corallum in *Halysites* (fig. 219) is fasciculate and reticulate, composed of long, tubular, cylindrical corallites, which are placed side by side in intersecting and anastomosing laminæ or lines, any given corallite being united with its neighbours to the right and left along its whole length, and each lamina of the corallum consisting of no more than a single linear series of tubes. Each tube is enclosed in a strong imperforate wall, surrounded on its free sides by a thick epitheca; and there may be a distinct division of the corallites into two series of different sizes, in which case a single small tube is placed between each pair of the larger tubes. In other cases all the tubes are similar in size and structure. Septa may be wanting, and, when present, have the form of vertically disposed rows of spines, in cycles of twelve. The tabulæ are complete, horizontal, or slightly concave, not vesicular, the smaller corallites (when present) being much more closely tabulate than the larger ones.

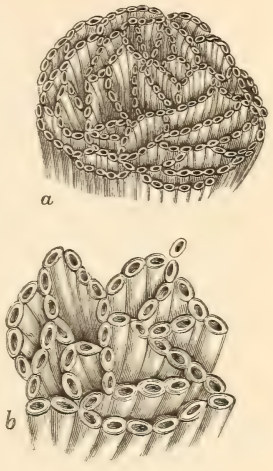

Fig. 219.—*a*, Upper surface of a fragment of *Halysites escharoides*, from the Silurian rocks of Canada, of the natural size; *b*, Part of the same enlarged. (Original.)

The species of *Halysites* may be divided into two groups, according as the corallum is composed throughout of corallites of one size, or consists of two sets of corallites of different sizes. The common *H. escharoides* of the Silurian rocks (fig. 219, and fig. 220, A) is an example of the forms in which all the corallites are similar. On the other hand, in the familiar *H. catenularia* of the same formation, the corallum consists of large corallites separated by the intervention of small, closely tabulate tubes (fig. 220, B and C). Septa are sometimes absent (fig. 220, B), but in other instances they are well developed (fig. 220, A). When present, the septa always have the form of vertical rows of spines, twelve of such rows being usually recognisable in each corallite. The mode of growth of the corallum is by "stolonal gemmation," the colony in its early condition being not unlike that of an *Aulopora*.

The zoological position of the genus *Halysites* cannot be regarded as certain, but it would appear, on the whole, to be most nearly

related to the *Heliolitidæ*. At the same time, there are indications of a possible relationship between *Halysites* and the *Syringoporidæ*. This is particularly shown by the peculiar coral described by Mr Etheridge from the Arctic Silurian rocks under the name of *Halysites catenulatus*, var. *Feildeni*, which has the *form* of *Halysites*, but

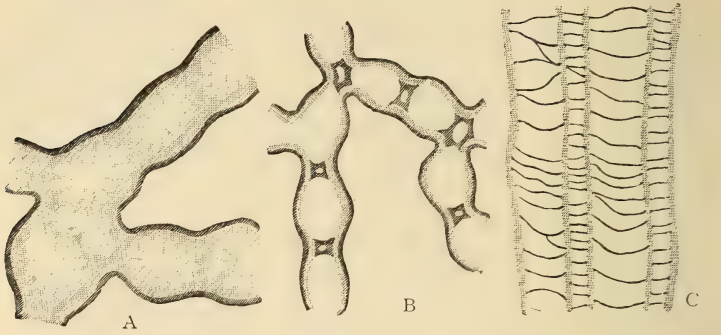

Fig. 220.—A, Transverse section of *Halysites escharoides*, Lam., from the Silurian of Gotland, enlarged ten times, showing the spiniform septa, and the absence of a series of small corallites; B, Transverse section of *Halysites catenularia*, Linn., from the Wenlock Limestone of Dudley, enlarged five times, showing the absence of septa, and the presence of a series of small corallites; C, Vertical section of a few corallites of the last specimen, enlarged five times, showing the large and small corallites, and the difference in the tabulation of these. (Original.)

in which the corallites resemble those of *Syringopora* in being furnished with connecting-tubes. This singular type cannot, however, be regarded as properly belonging to *Halysites*.

Tetradiidæ.

This small family includes only the single genus *Tetradium*, which, so far, has only been detected in the Ordovician rocks of North America. In this genus the corallum (fig. 221) is massive, and is composed of long, prismatic and closely contiguous corallites, which are of small size, and have imperforate walls. The tubes are furnished with longitudinal inflections or plications, generally four in number in each tube, which do not reach the centre of the visceral chamber, and which give a characteristic cruciform or petaloid aspect to cross-sections of the corallites (fig. 221, B). These longitudinal plications are apparently to be regarded as of the nature of septa or pseudosepta. The tubes are crossed by numerous tabulæ (fig. 221, C), which are sometimes complete, but are at other times perforated by central apertures (as in the tabulæ of some species of *Stenopora*). The mode of increase appears to be by fission.

Tetradium appears to be related to *Halysites*, but its true affinities and zoological position are uncertain.

CHÆTETIDÆ.

This family includes only the single genus *Chætetes*, all the known species of which are found in the Carboniferous rocks, though vari-

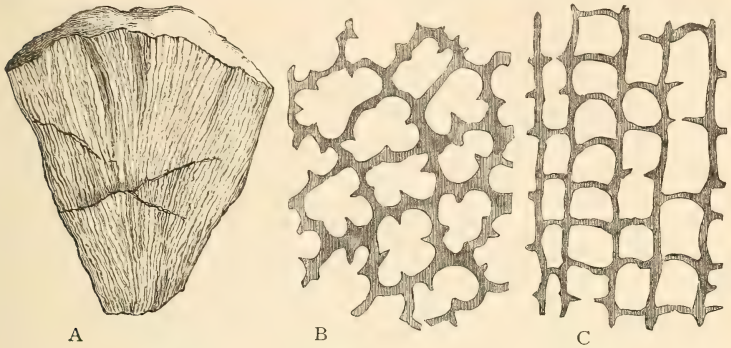

Fig. 221.—A, Fragment of a large corallum of *Tetradium minus*, Safford, from the Cincinnati Group of North America, of the natural size; B, Transverse section of the same, enlarged ten times, showing the petaloid form of the tubes and the short septa; C, Vertical section of the same, similarly enlarged, showing the tabulæ. (Original.)

ous Monticuliporoids have been formerly referred to the same genus. The type-species is the *C. radians* of the Carboniferous Limestone

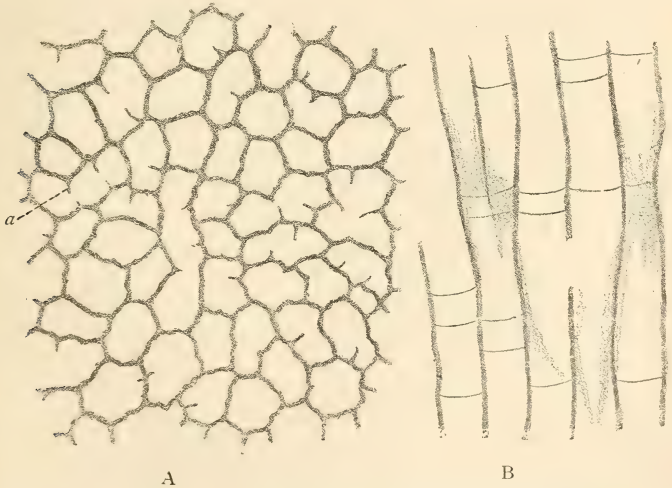

Fig. 222.—A, Tangential section of *Chætetes Etheridgii*, from the Carboniferous Limestone of Westmorland, enlarged about ten times; B, Longitudinal section of the same, similarly enlarged. *a*, Imperfect longitudinal partition produced by uncompleted fission of an old corallite. (Original.)

of Russia, but the characters of all the known species are essentially the same. The corallum in *Chætetes* is massive or laminar, often

of large size; and consists of long, tubular, prismatic corallites, which are not only in close contact throughout, but are so completely incorporated by fusion of their walls that rough fractures almost always expose the interior of the tubes. The corallites are all of one kind, are irregularly polygonal, and possess completely imperforate walls. The tubes are traversed by a few complete tabulæ (fig. 222, B), which are commonly developed periodically at successive levels; but there are no septa. The increase of the corallum is by fission of the old tubes; and hence in cross-sections (fig. 222, A) it is common to observe imperfect longitudinal partitions projecting into the visceral chambers of the corallites, and indicating the uncompleted fission of the tubes.

The zoological affinities of the genus *Chætetes* are quite uncertain, and it is not even clear that it is referable to the *Alcyonaria*. Many authorities regard the genus as belonging to the *Polyzoa* rather than to the *Cœlenterata;* but the fissiparous mode of its development, and the total absence of pores or canals connecting adjoining tubes, would militate strongly against its being referred to the former group.

Auloporidæ.

This small and imperfectly understood group comprises the Palæozoic genera *Aulopora*, *Cladochonus* (*Pyrgia*), and *Monilipora*, of which the first may be taken as the type. The corallum in *Aulopora* (fig. 223, A) has the form of a creeping, branched, or reticulate system of tubes, attached by the whole of the lower surface to the exterior of a shell, coral, or other foreign body. The prostrate stems or stolons send up at longer or shorter intervals reclined tubular or trumpet-shaped corallites, which are free terminally, and do not grow up to form a fasciculate mass. As regards their internal structure, the corallites are commonly furnished with curved or horizontal tabulæ, and rudimentary septa are present in the form of marginal striæ or rows of tubercles. The walls of the corallites are imperforate, and the mode of increase of the corallum is by stolonal gemmation. The species of *Aulopora* range from the Ordovician to the Carboniferous inclusive.

Cladochonus (*Pyrgia*) closely resembles *Aulopora*, but the colony is only attached to foreign bodies by isolated points of attachment, and grows in an erect manner rather than as a creeping network. In its young state, the corallum consists of a single trumpet-shaped corallite (fig. 223, C and D), attached by processes springing from its lower surface. *Monilopora* possesses an Auloporoid corallum, which is attached parasitically to the stems of Crinoids in a ring-like manner, the walls of the trumpet-shaped corallites having a peculiar

cancellated structure. Both these genera are confined to the Carboniferous period.

The true relationships of the *Auloporidæ* are uncertain. A close resemblance exists between the adult colonies of *Aulopora* and the young stages of both *Syringopora* and *Halysites*, but it is questionable

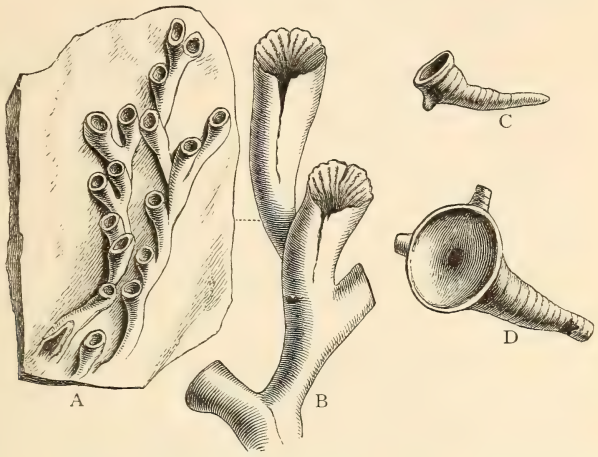

Fig. 223.—A, Portion of *Aulopora tubæformis*, of the natural size; and B, Portion of the same, enlarged (after Goldfuss). Devonian. C and D, *Cladochonus* (*Pyrgia*) *Michelini*, of the natural size, and enlarged (after Milne-Edwards and Haime). Carboniferous.

if this likeness bespeaks any real affinity to either of these genera. In the stolonal method of gemmation characteristic of the Auloporoids we have a marked Alcyonarian feature, and the group may therefore be provisionally placed in the division of the *Alcyonaria*.

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CHAPTER XXI.

THE MONTICULIPOROIDS.

We may consider here the remarkable groups of organisms (*Monticuliporidæ* and *Fistuliporidæ*), which have been collectively spoken of as the "Monticuliporoids," and the precise systematic position of which is still uncertain. The Monticuliporoids, in fact, exhibit a combination of characters; and palæontologists have therefore, so far, come to no final decision as to the true relationships of these puzzling organisms, some authorities regarding them as a peculiar group of Corals, while others consider them to be referable to the *Polyzoa*.

The structural characters of the Monticuliporoids are very complex, and are for the most part only capable of complete elucidation by means of microscopic examination, while the number of different forms included in the group is very large. For these reasons, nothing more will be here attempted than to give a brief outline of the general morphology of the entire series, with the distinctive characters of the two families of the *Monticuliporidæ* and *Fistuliporidæ*, and a brief notice of the more important types included in these.

In all the Monticuliporoids, the skeleton is composed of closely approximated, prismatic or sub-circular tubes, sometimes all similar to one another, sometimes of different sizes, which are provided with distinct walls. In the centre of the colony the tubes are always thin-walled, more or less polygonal in shape, and similar to one another in internal structure; but as they approach the surface, they diverge from one another by the intercalation of new tubes, their walls commonly becoming at the same time thickened, and their internal characters being modified. It is in the outer, or "mature," region of the colony (fig. 224, E, *m*) that a second set of tubes is usually developed in those cases in which the colony is dimorphic. The exterior of the colony commonly exhibits at intervals definite areas ("monticules" and "maculæ"), which are elevated or depressed as regards the general surface, and consist of larger or smaller tubes

than the average (fig. 224, *mo*). The walls of the tubes are imperforate; tabulæ are always present; and true "septa" are probably always wanting, though "pseudosepta," in the form of radial plates or spines, are in rare cases developed.

The *form* of the skeleton in the Monticuliporoids is extremely variable, though it is in general tolerably constant for each species. In many forms the skeleton is dendroid or ramose (fig. 224, B), consisting of cylindrical or subcylindrical stems, which have a fixed base and branch more or less freely above, the entire surface being covered with the openings of the tubes. In others, the skeleton is so far modified from the preceding that it assumes the form of an erect, laminar or frondescent

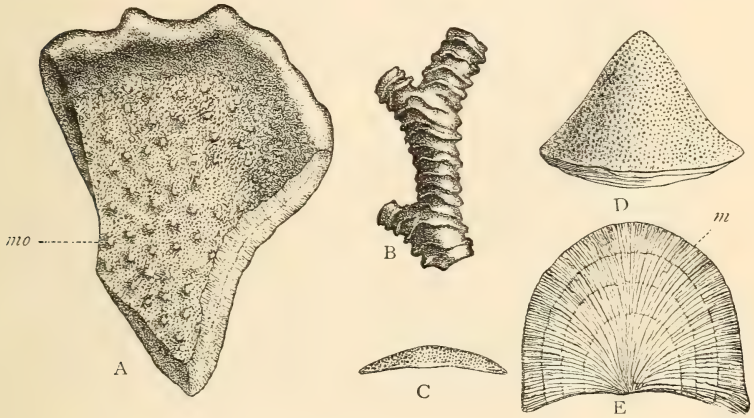

Fig. 224.—A, Fragment of the frondescent corallum of *Monticulipora mammulata*, D'Orb. (=*Peronopora molesta*, Nich.) showing "monticules" (*mo*); B, Fragment of the dendroid corallum of *Callopora?* (*Heterotrypa*) *rugosa*, E. and H.; C, Discoid corallum of *Amplexopora discoidea*, James; D, Hemispherical corallum of *Callopora nummiformis*, Dyb., viewed sideways; E, The same vertically fractured, showing the divergence of the tubes and the peripheral "mature" region (*m*). All the figures are of the natural size, except E, which is reduced. (Original.)

colony, composed of two strata of tubes the mouths of which open on the two sides of the expansion (fig. 224, A). In numerous other types (fig. 224, D) the colony is hemispherical, the usually flattened or concave base being covered with a concentrically wrinkled epitheca, while the mouths of the tubes cover the entire upper surface. In still other forms, the tubes are very short, and the colony has the form of a thin, flat or concave disc, with a striated basal plate (fig. 224, C). In other cases, the skeleton assumes a lobate or massive form; and in others it is encrusting, and is attached parasitically to foreign bodies.

A very important distinction between different types of the Monticuliporoids is based upon the homomorphic or heteromorphic condition of the colony. In some forms (viz., in *Monotrypa*) the tubes are essentially similar throughout the colony in size and internal structure, any difference which may be observed between different

tubes appearing to depend upon their relative age only. On the other hand, most Monticuliporoids exhibit a distinct dimorphism, the colony being composed of at least two kinds of tubes, which differ in size and in internal structure. The relative proportions of these two sets of tubes to one another vary in different forms, but the larger ones may be spoken of as "autopores," and the smaller ones as "mesopores." The "autopores" may be regarded as having lodged the perfect zoöids of the colony, and they are distinguished both by their comparatively large size (fig. 225, *a*), and also by the nature of their tabulæ, these structures being usually comparatively

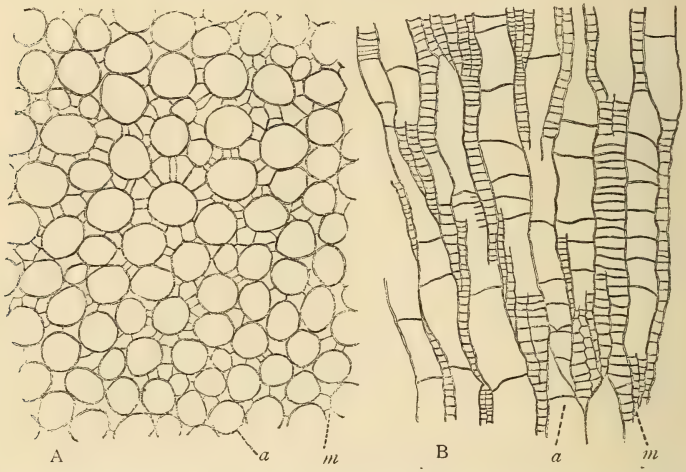

Fig. 225.—A, Tangential section of *Callopora nummiformis*, Dyb., from the Silurian rocks of Esthonia, enlarged twenty times; B, Vertical section of the same, similarly enlarged. *a*, Autopore; *m*, Mesopore. (Original.)

few and remote, or being specially modified in form. On the other hand, the "mesopores," or "interstitial tubes," occupy, in greater or less number, the spaces between the autopores, and are not only smaller than the latter, but are more closely tabulate (fig. 225, *m*). The mesopores have often been considered as merely of the nature of a "cœnenchymal" or "interstitial" tissue, but they may be regarded, with great probability, as really having lodged imperfect zoöids, and as corresponding with the "siphonopores" of the *Helioporidæ* and *Heliolitidæ*.

In addition to the preceding, many Monticuliporoids—whether otherwise homomorphic or heteromorphic—possess yet a further series of tubes, which have been spoken of as "acanthopores" or "spiniform corallites." These are minute cylindrical tubes, with thick and laminated walls (fig. 226), which run in the substance of

the walls bounding contiguous autopores or mesopores, and the free ends of which usually project above the general surface as spines or blunt tubercles (fig. 227). The "acanthopores," when present, are only developed in the peripheral or "mature" region of the colony; and they are readily recognised in tangential sections (fig. 226, *ac*), as round bodies which usually show a minute central tube surrounded by a thick and dark-coloured wall of laminated calcareous tissue. Waagen has expressed the opinion that the "acanthopores" are only immature tubes, but this is conclusively shown to be erroneous by the fact that, while immature tubes can be readily demonstrated in *all* specimens, the "acanthopores" are strictly confined to particular *species* of Monticuliporoids, and are uniformly absent in others.

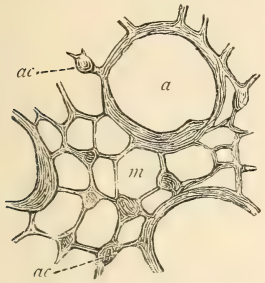

Fig. 226.—A few corallites of *Fistulipora eriensis*, Rom.: *a*, Autopores; *m*, Mesopores; *ac*, Acanthopores. Enlarged about forty times.

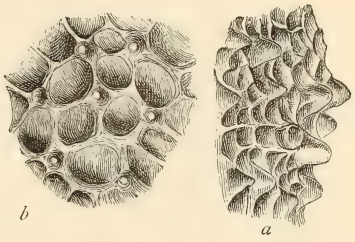

Fig. 227.—*a*, Profile view of a portion of the surface of *Dekayia aspera*, showing acanthopores; *b*, The same, viewed from above. Enlarged about forty times. (After Nicholson and Foord.)

Moreover, they differ entirely in structure from the young tubes, and unlike the corallites (whether young or old) they project above the general surface of the colony in the form of spines. Again, when they are limited in number, the acanthopores occupy definite positions as regards the ordinary tubes of the colony; and, finally, in many forms (fig. 230, D) the acanthopores are so numerous as to render the hypothesis that they are of the nature of young corallites quite untenable. It may, then, be taken as certain that the acanthopores represent a special morphological element in the Monticuliporoid colony; but it is difficult to give any satisfactory explanation as to their true nature. They may be regarded, with considerable probability, as of the nature of aborted zoöids; and possibly their nearest analogue is to be found in the "avicularia" of the recent *Polyzoa*. This suggestion is supported by the fact that in some living Polyzoans (as in *Retepora*) the avicularia are attached to thickened tubes immersed in the substance of the skeleton, the appearance of which in thin sections is very similar to that observed in sections of those Monticuliporoids which possess acanthopores.

In many Monticuliporoids the surface is studded at intervals with small elevations which are known as "monticules" (fig. 224, A), and which are usually constituted by groups of corallites of larger than the average size. In other cases, there are scattered depressed areas, usually stellate in form, which are occupied by the "mesopores" only, and which are known as "maculæ." These can be shown to be really of the nature of centres of growth for the colony.

So far as is certainly known, the walls of the tubes in the Monticuliporoids are wholly destitute of mural pores, or foramina of any kind, the chambers of contiguous tubes being thus completely separated from one another. Considering the vast number of thin

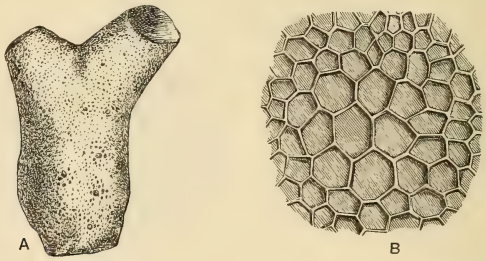

Fig. 228.—A, Part of a typical specimen of *Monotrypella pulchella*, E. and H., from the Wenlock Limestone of Dudley, of the natural size; B, Part of the surface of the same, embracing one of the clusters of large corallites, enlarged. (Original.)

sections of the Monticuliporoids which have been examined by competent observers, the imperforate condition of the walls of the tubes in the Monticuliporoids must be regarded as free from doubt; and it constitutes one of the most marked features by which these organisms are separated from the Cyclostomatous *Polyzoa*. Mural pores have been described by De Koninck, and also by the present writer and Mr R. Etheridge, jun., as occurring in the genus *Stenopora;* but the exhaustive investigations of Waagen and Wentzel have shown that even in this genus the walls are really imperforate, and that the structures described as pores in such forms as *Stenopora Jackii* must admit of a different interpretation. Mr Ulrich has also described pores as occurring in a Monticuliporoid, but it may be suggested with much probability that, in this case, the organism observed is really referable to some other group.

In almost all the Monticuliporoids the tubes are crossed by transverse calcareous partitions or "tabulæ," which are in general very numerous (fig. 225, B), though occasionally limited in their development. Usually, in the dimorphic forms, the autopores have few and remote tabulæ, while the mesopores have a much greater abundance of these structures. Mostly, the tabulæ are "complete," forming horizontal partitions which extend entirely across the tubes (fig.

225, B). In other cases, one half of the tube is crossed by straight tabulæ, while the other half is occupied by curved or "cystoid" tabulæ, forming a series of lenticular vesicles on one side (fig. 230, F). In other cases (*Prasopora*), "cystoid" tabulæ are developed all round the periphery of the tube, and the centre is occupied by straight tabulæ. Lastly, in *Fistulipora*, the walls of the mesopores are incompletely developed, and the tabulæ unite to form a tissue of lenticular vesicles between the autopores, the genus thus bearing the same relation, in this respect, to *Callopora* that *Plasmopora* does to *Heliolites* among the *Heliolitidæ*.

The great majority of the Monticuliporoids exhibit no radial structures in the tubes which could be compared with the "septa" of an ordinary coral. In a few forms, such structures do occur, but it is doubtful if in any such instance we have to deal with structures really developed in mesenteries, and therefore really homologous with the "septa" of the *Zoantharia*. Thus in *Fistulipora*, each autopore is provided with two longitudinal folds, situated opposite one another, towards one end of the visceral chamber. Again, in a hitherto undescribed species of *Callopora* (fig. 229, A) each

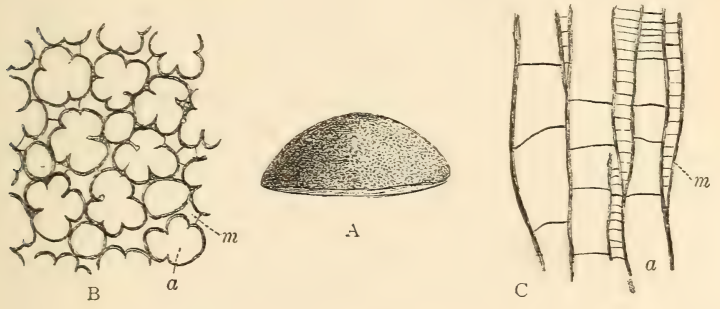

Fig. 229.—A, A large specimen of *Callopora Foordii*, of the natural size; B, Tangential section of the same, showing the pseudoseptal folds in the autopores, enlarged twenty times; C, Vertical section of the same, similarly enlarged. *a*, Autopores; *m*, Mesopores. From the Ordovician rocks of Esthonia. (Original.)

autopore is provided with from two to five radial plications of the wall, which closely resemble the "septa" of *Tetradium*, and give a characteristic floriform appearance to cross-sections of the corallites. Moreover, in typical examples of *Monticulipora mammulata*, D'Orb. (= *Peronopora molesta*, Nich.), the author has detected radially disposed spines (fig. 230, D), which have much the appearance of the radial spines of *Favosites* and *Syringopora*; and similar structures have been recognised by other observers in other forms.

Lastly, as regards the *mode of growth* of the skeleton, new tubes are most usually produced by "intermural gemmation," in a manner

precisely similar to that which obtains in the *Favositidæ*. It is for this reason that rough fractures of the Monticuliporoids expose the *walls* of tubes, whereas in the genus *Chætetes*, where the growth is fissiparous, fractures usually lay open the visceral chambers of the corallites. It is, however, interesting to note that *fission* also occurs not rarely in the Monticuliporoids, though it is not so common a mode of increase as gemmation. In the mesopores of *Fistulipora* and some allied types fission seems to be the ordinary mode of increase, as it is in the case of the siphonopores of the *Heliolitidæ*. This fact would go far to prove that the mesopores are not merely cœnenchymal; since fission can hardly occur unless we suppose the existence of separate zoöids endowed with the power of division. The occurrence of fission in the autopores of the Monticuliporoids is also strongly against the reference of these organisms to the Cyclostomatous *Polyzoa*, since these latter invariably increase by means of gemmation. A still more interesting fact is the occurrence—as described by Waagen—of "cœnenchymal gemmation" among the Fistuliporoids, autopores in these cases being formed by the abortion and apparent fusion of a group of mesopores, in a manner precisely similar to that previously noted as occurring in *Heliopora* and *Heliolites*. This fact would also bear very strongly against the view that the Monticuliporoids are to be regarded as belonging to the *Polyzoa*.

It must be admitted, however, that the *zoological affinities* of the Monticuliporoids are still a matter of uncertainty. In many of their features, both structural and developmental, they show marked relationships with the *Actinozoa* generally, and with the *Alcyonaria* in particular, while in others they approach the *Polyzoa;* and it must, in the meanwhile, remain a matter of individual opinion whether the Monticuliporoids should be regarded as a very peculiar group of Corals or as an equally peculiar group of Polyzoans. It would be out of place here to enter into any detailed discussion of a question so complex, but it may be of advantage to summarise briefly the chief points which must be taken into consideration in coming to any decision as to the systematic position of the Monticuliporoids.

Leaving the *external form* of the skeleton entirely out of consideration, the *general* features which favour the reference of the Monticuliporoids to the *Cœlenterata* are the following:—

1. The common dimorphism of the colony in the Monticuliporoids finds its best parallel in *Heliopora* and *Heliolites*, the Cœlenterate nature of which is undoubted. In particular, the structural relationships between *Fistulipora* and *Heliolites*, or *Plasmopora*, are exceedingly close; the skeleton consisting in both of large, sparsely tabulate tubes ("autopores") separated by smaller, closely tabulate tubes ("mesopores" or "siphonopores"), and the former of these possessing radial structures of the nature of "septa" or "pseudosepta."

2. The Monticuliporoids increase by fission as well as by gemmation, whereas the recent *Polyzoa* appear to be uniformly characterised by a gemmiparous mode of development, which varies in its precise details in different groups. Moreover, the gemmation of the Monticuliporoids is "intermural," and is precisely similar to that which obtains among the *Favositidæ*.

3. "Cœnenchymal gemmation" occurs in the *Fistuliporidæ*, this mode of increase being otherwise absolutely characteristic of *Heliopora* and of the *Heliolitidæ*.

4. The walls of the tubes in the Monticuliporoids are imperforate; whereas in the calcareous *Polyzoa* the skeleton seems to be almost always (probably always) porous, and the cavities of contiguous cells are usually placed in direct communication by means of connecting-foramina or tubes.

5. The abundant development of "tabulæ" in the Monticuliporoids is a feature in which these organisms resemble a large number of undoubted Corals.

6. Certain Monticuliporoids possess in their autopores radial folds or plications which may be compared with the "pseudosepta" of *Heliopora;* while others (*Monticulipora mammulata*) possess radially disposed calcareous spines, which are closely similar to the septal spines of *Favosites*, of *Syringopora*, and of certain species of *Heliolites*.

On the other hand, there are the following considerations which would point to a relationship between the Monticuliporoids and the *Polyzoa*, or which, at any rate, would more or less diminish the importance of some of the features above mentioned as showing the Cœlenterate affinities of these organisms.

1. The polyzoary of *Heteropora* (which is undoubtedly a Polyzoan) consists of large tubes scattered among smaller ones, though there does not appear to be any essential difference in the *structure* of these respectively.

2. "Tabulæ" are by no means confined to the Cœlenterates, precisely similar structures—so far as appearance goes—being present in undoubted *Polyzoa* (*e.g.*, in *Heteropora, Domopora, Fascicularia, Alveolaria*, &c.)

3. Radial structures in the form of rows of spines are present in a number of *Polyzoa* (*e.g.*, in *Heteropora, Discoporella*, &c.)

4. There are various *Polyzoa* (such as *Rhombopora Hamiltonensis*, *Ceriopora interporosa*, and some of the Fenestellids) which possess structures apparently very similar to the "acanthopores" of many Monticuliporoids. Structures presenting in some respects the same aspect are found in the recent *Reteporæ*, in which they serve to carry the avicularia.

5. Portions of the skeleton of *Fistulipora incrustans*, Phill., have been shown by John Young to become thickened, and to exhibit a finely tubulated structure similar to that seen in the skeleton of the *Fenestellidæ*.

6. According to the observations of Lindström, certain of the Monticuliporoids pass through early stages of development in which the skeleton is of a distinctly Polyzoan type. As an example of this, we may take the singular *Callopora heterosolen*, the basal (and therefore first-formed) portion of which exhibits Polyzoan characters, while the main mass of the skeleton is of the ordinary Monticuliporoid type.

7. Lastly, certain extinct forms the Polyzoan nature of which seems unquestionable are hardly distinguishable, as regards minute structure, from other forms which have always been regarded as Monticuliporoids. Thus, an extremely close structural resemblance obtains between *Ceriopora interporosa*, on the one hand, and *Batostomella* (*Monticulipora*) *tumida*, on the other hand.

As regards their *geological distribution*, the forms usually regarded as Monticuliporoids are exclusively Palæozoic, and range from the Ordovician to the Permian inclusive. In the Ordovician rocks, in particular, Monticuliporoids are enormously abundant, and they also constitute a conspicuous feature in the Silurian deposits, while their number is much reduced in the Devonian, Carboniferous, and Permian strata. As a rule, particular types are confined to special geological horizons, but the vertical distribution of the group still requires to be worked out in detail. So far as certainly known, the genus *Stenopora*—a name which has served to cover many different types of the Monticuliporoids—is confined exclusively to the Carboniferous and Permian deposits. It is not at all improbable that representatives of the Monticuliporoids will be found to have survived into the Secondary period, while there are even Tertiary fossils which show remarkable points of resemblance to this ancient group of organisms.

With regard to the *classification* of the Monticuliporoids, two principal types of structure may be recognised, represented respectively by the genera *Monticulipora* and *Fistulipora*, as these are now restricted. These two types of structure may be taken with convenience as the foundation of the two families of the *Monticuliporidæ* and *Fistuliporidæ*. It must be admitted, however, that these two families are connected together by transitional forms; and it is probably impossible, in the present state of our knowledge, to so define them as to render them mutually exclusive.

Monticuliporidæ.

The skeleton of the *Monticuliporidæ* is very variable in form, and may be either composed of essentially similar tubes throughout, or may be made up of large tubes ("autopores") and of a limited number of smaller, closely tabulate tubes ("mesopores"). The interstitial tubes or "mesopores" are not sufficiently developed to isolate the autopores, while they are provided with complete walls and their tabulæ are straight. "Acanthopores" are very commonly present. Septal spines are rarely developed. The mode of growth of the skeleton is by intermural gemmation, commonly associated with fission.

This family includes the genera *Monticulipora*, *Monotrypa*, *Mono-*

trypella, *Dianulites*, *Diplotrypa*, *Dekayia*, *Stenopora*, &c., and ranges from the Ordovician to the Permian period.

The type of the genus *Monticulipora* is the *M. mammulata*, D'Orb., of the Ordovician rocks of North America, which Mr Ulrich identifies with the form described by the writer under the name of *Peronopora molesta*. In this form, the corallum (fig. 224, A) has usually the shape of a laminar erect expansion, composed of two layers of tubes which open on the two sides of the frond. The large tubes or "autopores" are placed close together, and just before reaching the surface their walls become

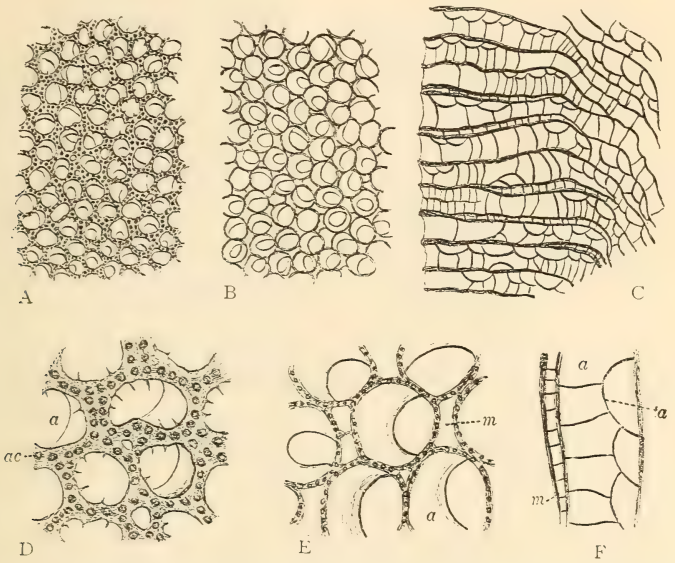

Fig. 230.—Morphology of *Monticulipora mammulata*, D'Orb. (=*Peronopora molesta*, Nich.), Ordovician, Cincinnati. A, Tangential section taken immediately below the surface, enlarged twenty times. B, Tangential section taken at a greater depth below the surface, similarly enlarged. C, Vertical section, showing one side of the double frond, similarly enlarged. D, E, and F, Portions of the preceding sections enlarged forty times: *a*, Autopores; *m*, Mesopores; *ac*, Acanthopores; *ta*, One of the "cystoid" tabulæ of an autopore, the rest of the tube being crossed by straight tabulæ. (Original.)

considerably thickened; hence there is a considerable difference between sections taken just below the actual surface (fig. 230, A and D) and those taken at a little depth (fig. 230, B and E). Interstitial tubes or mesopores are developed in small number, and are easily recognised in long sections by their close tabulation (fig. 230, F). Acanthopores are developed in great numbers, and form a ring round each autopore (fig. 230, D), but they are difficult to recognise except in tangential sections taken close to the surface. The autopores are furnished with two sets of tabulæ, each tube showing a series of vesicular or "cystoid" tabulæ on one side (fig. 230, F, *ta*) with a series of straight tabulæ in the other half of the tube. Owing to this peculiarity in the tabulation of the autopores, tangential sections (fig. 230, B) exhibit the cut edges of the cystoid tabulæ in the

form of a curved or horse-shoe-shaped line in the interior of each autopore. In some examples of this species, the autopores are provided with radially disposed pseudoseptal spines (fig. 230, D), but these are not recognisable in other specimens.

Of the remaining genera of the *Monticuliporidæ* only two or three can be briefly noticed here. The genus *Monotrypa* is characterised by the fact that the tubes are essentially similar to one another, being polygonal, thin-walled, and furnished with few remote tabulæ, while mesopores are absent, as, usually, are acanthopores also. The genus ranges from the Ordovician into the Devonian. *Monotrypella* is very similar to *Monotrypa*, but the corallites become thickened by stereoplasma as they approach the surface, their walls, however, always remaining distinct (fig. 231).

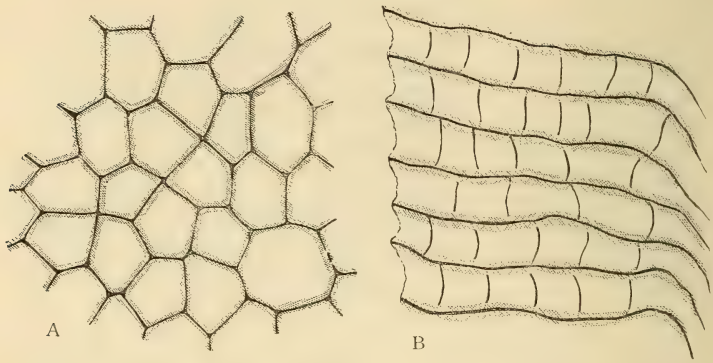

Fig. 231.—Sections of *Monotrypella pulchella*, E. and H., from the Wenlock Limestone of Britain, enlarged about eighteen times. A, Tangential section; B, Longitudinal section. (Original.)

The Ordovician genus *Dianulites* (as based upon *Dianulites fastigiatus*, Eichw.) is essentially similar to *Monotrypa* as regards the nature and structure of the corallites, but the corallum is inversely conical in form, and is provided with a striated epithecal membrane, so that the calices open at the upper end of the colony only, and the organism is superficially quite like a simple coral in appearance. The genus *Amplexopora*, ranging from the Ordovician to the Carboniferous, nearly resembles *Monotrypella* in structure; but numerous acanthopores are developed, which often form complete rings round the autopores. *Dekayia*, again, resembles *Monotrypella* in having only a single set of tubes, without mesopores, but the walls of the autopores are united, and there are numerous large acanthopores, the apices of which project above the surface as prominent blunt spines (fig. 227). The genus is only known from the Ordovician rocks.

Lastly, in the Carboniferous and Permian genus *Stenopora*, the colony consists of oval or circular or subpolygonal autopores, the walls of which on approaching the surface become thickened with annular deposits of stereoplasma, which are separated by unthickened nodes (fig. 232, C), this peculiarity giving a very characteristic appearance to longitudinal sections. In the centre of the colony the corallites are polygonal and thin-walled, and do not exhibit the characteristic annulations of the genus.

Mesopores are not developed, but there are usually numerous acanthopores (fig. 232, A and B). The tabulæ are usually straight and complete, but they are sometimes perforated by central apertures (fig. 232, C). The walls of the autopores in *Stenopora* have been described as being perforated by mural pores, but, as previously noted, the researches of

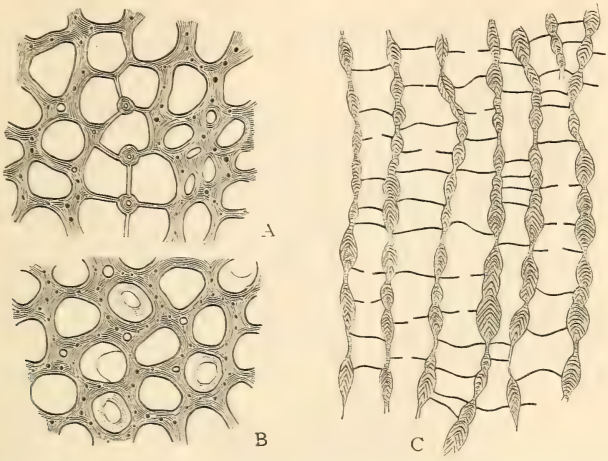

Fig. 232.—Sections of *Stenopora Howsii*, from the Carboniferous rocks of England, enlarged about eighteen times. A and B, Tangential sections; C, Longitudinal section, showing the periodic thickenings of the walls of the tubes. (Original.)

Waagen and Wentzel have rendered it certain that the supposed mural pores must be otherwise explained, and that the walls of the tubes are really imperforate.

FISTULIPORIDÆ.

The skeleton in this family is of very variable form, and is composed of large tubes ("autopores") which are in general more or less completely isolated (fig. 233) by the development of a copious series of smaller tubes ("mesopores"), these latter being often aggregated into star-shaped groups or "maculæ," which serve as centres of growth for the colony. The walls of the autopores are either completely unthickened (*Callopora* and *Prasopora*), or are specially thickened on one side (*Fistulipora*). The mesopores are furnished with more numerous tabulæ than the autopores; and in some cases (*Fistulipora*) their walls are incomplete, thus allowing their tabulæ to coalesce so as to form an interstitial tissue of lenticular vesicles. The mode of increase as regards the autopores is typically by "cœnenchymal gemmation," the mesopores increasing by means of fission. Pseudoseptal spines are occasionally developed, and pseudoseptal folds are commonly present. Acanthopores are occasionally, but not usually, developed.

Since "cœnenchymal gemmation" is at present only known as occurring (apart from the present family) in the unquestionably Actinozoan groups of the *Helioporidæ* and *Heliolitidæ*, it would seem that the presence of this mode of increase in the Fistuliporoids, first pointed out by Waagen, is an almost incontrovertible proof that the latter should be referred to the Alcyonarian Zoophytes. If this be admitted, however, it would follow, almost inevitably, that the *Monticuliporidæ* should also be regarded as Alcyonarians, since there exists an exceedingly close relationship between these and the Fistuliporoids. No arrangement, in fact, which would refer *Fistulipora* and *Callopora* to one great division of the animal kingdom (*Cœlenterata*), and would place *Monticulipora*, *Diplotrypa*, and allied types in another great division (*Polyzoa*) could possibly be sustained.

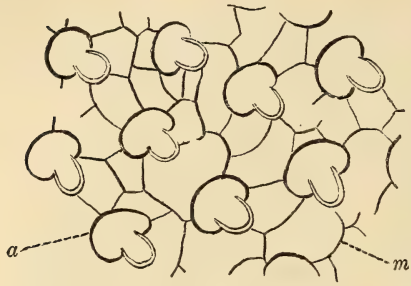

Fig. 233.—Tangential section of *Fistulipora trifoliata*, from the Middle Devonian of Gerolstein, enlarged about forty times, showing the trifoliate autopores (*a*) and the interstitial mesopores (*m*). (After Nicholson and Foord.)

The type-genus of the Fistuliporoids is *Fistulipora* itself, in which the variously shaped corallum is composed of oval or cylindrical autopores, which are furnished towards one side with two longitudinal folds ("pseudosepta"), giving to the tubes in cross-sections a characteristic bilobed or trifoliate appearance (fig. 233), and which are separated by one or more rows of mesopores (fig. 234, D). The walls of the mesopores are ncompletely developed, and their tabulæ therefore coalesce to give rise ɔ a vesicular tissue occupying the spaces between the autopores (fig. 234, E). Acanthopores are occasionally developed, and in some cases pseudoseptal spines have been observed.

The species of *Fistulipora* are Silurian, Devonian, and Carboniferous, and are in general readily recognised by the trifoliate form of the autopores in cross-sections, the abundance of the mesopores, and the fact that the tabulæ of the mesopores coalesce to form a tissue of lenticular vesicles occupying the spaces between the autopores, and resembling the similarly formed vesicles which separate the autopores in *Plasmopora* and *Propora*. In some forms, the two pseudoseptal folds which are so characteristic of the genus are little developed (compare fig. 234, D, with fig. 233), and the trifoliate shape of the tubes is proportionately obscured. The peculiar horse-shoe-shaped sinus along one side of the autopores, formed by the pseudosepta, has been considered, with much probability, as corresponding in the living animal with a ciliated groove ("siphonoglyphe") such as is found in the œsophagus of the Alcyonarians. Another characteristic feature in many species of the genus is that the portion of the wall bounding the sinus just spoken of is considerably thickened, and

in well-preserved specimens sometimes exhibits a peculiar striated aspect, as if it were finely tubulated.

The genus *Callopora*, as maintained by Waagen, must find a place in the immediate neighbourhood of *Fistulipora*. The typical species of this genus resemble *Fistulipora* in most respects, but the autopores are, as a rule, without pseudoseptal folds, and the mesopores have complete walls and are furnished with straight tabulæ, which do not coalesce to form an interstitial vesicular tissue (fig. 225, B). In some cases, traces of pseudo-

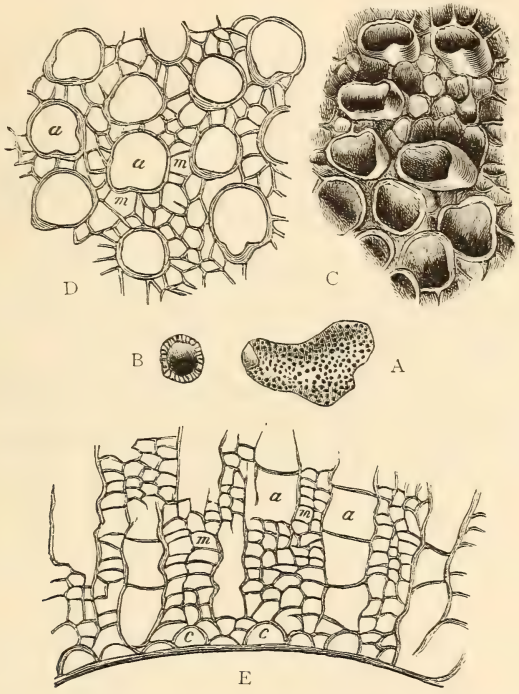

Fig. 234.—*Fistulipora incrustans*, from the Carboniferous rocks of England. A, A colony growing on the stem of a Crinoid, of natural size; B, Broken extremity of the same, showing the thickness of the colony; C, Portion of the surface, enlarged almost twenty times; D. Tangential section, similarly enlarged; E, Vertical section, similarly enlarged. *a*, Autopores; *m*, Mesopores; *c*, Primordial tubes of the colony. (After Nicholson and Foord.)

septa are present in the autopores, and in one species (*Callopora Foordii*, fig. 229) these structures are exceptionally developed. Pseudoseptal spines are occasionally present in this genus. The walls of the autopores in *Callopora* are not specially thickened in the "mature" region of the corallum, as is shown by the structure of the type-species of the genus (*Callopora elegantula*, Hall). Hence, forms like *Callopora* (*?*) *ramosa*, E. and H., of the Ordovician rocks of North America, which have been referred here by Mr Ulrich, must find a place elsewhere, as the autopores become markedly thickened in the peripheral portion of the corallum.

The species of *Callopora* appear to be confined to the Ordovician and Silurian rocks.

Lastly, the Ordovician genus *Prasopora* differs from *Callopora* mainly in the fact that the autopores are furnished marginally with a series of vesicular or "cystoid" tabulæ, which enclose a central area traversed by straight tabulæ.

LITERATURE OF MONTICULIPOROIDS.

1. "Polypiers Fossiles des Terrains Paléozoiques." Milne-Edwards and Haime. 1851.
2. "Die Chætetiden der ostbaltischen Silurformation." Dybowski. 1877.
3. "On the Structure and Affinities of the Genus Monticulipora and its Subgenera." Nicholson. 1881.
4. "American Palæozoic Bryozoa." Ulrich. (A series of papers in the 'Journal of the Cincinnati Society of Natural History,' 1879-1884).
5. "Contributions to the Micro-Palæontology of the Cambro-Silurian Rocks of Canada." Foord. 1883.
6. "On the Genus Fistulipora, M'Coy, with Descriptions of several species." 'Annals and Magazine of Nat. Hist.' 1885. Nicholson and Foord.
7. "On the Tasmanian and Australian Species of the Genus Stenopora, Lonsdale." 'Annals and Magazine of Nat. Hist.' 1886. Nicholson and Etheridge, jun.
8. "The Salt-Range Fossils—Cœlenterata." 'Palæontologia Indica. 1886. Waagen and Wentzel.

CHAPTER XXII.

SUB-KINGDOM IV.—ECHINODERMATA.

General Characters of the Echinodermata.

The sub-kingdom of the *Echinodermata* comprises the animals usually known as Sea-urchins, Star-fishes, Brittle-stars, Sea-cucumbers, Sea-lilies, &c., and may be briefly defined as follows:—

Simple marine organisms, which are mostly bilaterally symmetrical when young, but which in the adult condition have this bilateral symmetry more or less extensively masked by a radial (usually pentamerous) arrangement of their parts. An alimentary canal is present, with or without a distinct anus, separate from the proper body-cavity. A system of water-vessels, often communicating directly with the exterior, and generally connected with protrusible tubes ("feet"), is present. The nervous system is radiate, consisting of an œsophageal ring and radiating branches. The integument is characteristically hardened by the deposition in it of carbonate of lime in the form of plates, granules, or spicules.

The adult Echinoderms always exhibit a more or less conspicuous radiate structure, the symmetry of the body being essentially pentamerous; but the larval forms are usually distinctly bilateral, and bilateral symmetry is in general more or less clearly recognisable in the fully grown animal. The radial symmetry of the body of the adult is exhibited not only in the external skeleton, but also in many of the internal organs, and especially in the nervous and ambulacral systems. The alimentary canal, unlike that of the Cœlenterates, is always completely shut off from the general cavity of the body, a mouth being always present, and an anal aperture usually existing as well. When a mouth and anus are present, these openings may be at opposite poles or on the same side of the body, the mouth being usually central in position, while the anus may be completely excentric. In the free-living Echinoderms, the mouth is usually either terminal and placed in front, or is situated in the centre of the in-

ferior surface of the body. On the other hand, in the stalked Crinoids and certain other forms, the ventral surface is directed upwards, and the mouth is thus placed on the superior aspect of the body.

Among the most characteristic of all Echinodermal structures are the so-called "water-vessels" or "ambulacral" vessels. This system consists of a series of musculo-membranous tubes filled with a watery fluid, and connected with the function of respiration, while at the same time commonly subserving locomotion. It consists essentially (fig. 235) of a circular vessel which surrounds the commencement of the alimentary canal, and gives off secondary vessels in a radiating manner. The "radiating vessels" usually give off at right angles numerous short lateral tubes (the "tube-feet" or "pedicels"); and the "circular vessel" is generally placed in communication with the exterior by a special canal ("stone-canal" or "water-tube") which opens on the surface by a spongy calcareous plate ("madreporite"). Though commonly subserving locomotion, the ambulacral vessels are probably primarily respiratory in function; and they not uncommonly give off leaf-like or branched external processes ("ambulacral gills"), which serve as respiratory organs. There is also a second vascular system, consisting of an oral ring and radial trunks, which are situated between the water-vessels and the nerve-bands. The oral ring is in relation with a peculiar organ, formerly described as a heart, but probably to be regarded as a kidney, which in many Echinoderms seems to communicate with the exterior by means of the madreporite.

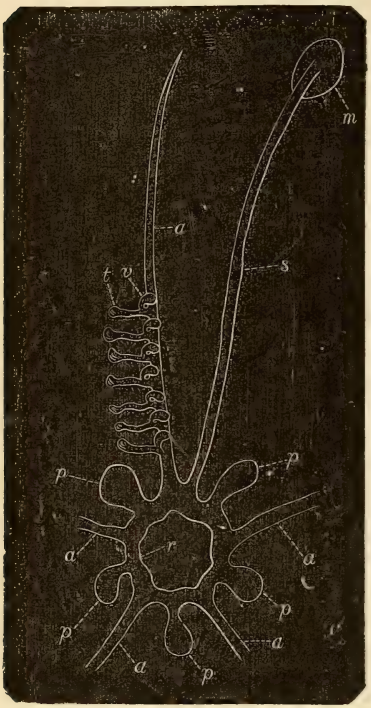

Fig. 235.—Diagram of tne ambulacral system of *Echinus*. *m*, Madreporite; *s*, Stone-canal; *r*, Central œsophageal ring; *p p*, Polian vesicles; *a a*, Radiating ambulacral vessels. Only the bases of four of the radiating vessels are shown; and a few of the tube-feet (*t*), with their secondary vesicles or "ampullæ" (*v*), are shown on one side of one of the radiating canals.

The sexes are almost always distinct in the Echinoderms, and the reproductive organs are usually lodged in the interior of the body, definite openings for the escape of the generative elements existing

in the body-wall. In the Crinoids, on the other hand, the reproductive organs are lodged in the "arms," and permanent generative apertures are rarely, if ever, present. As regards their position, the generative glands (ovaries or testes) alternate in the Echinoderms generally with the radiating nerve-cords and ambulacral vessels, and are therefore "interradial," while the latter are "radial"; but in the Crinoids the genital cord, being lodged in the arms, is necessarily radial in position.

The integument of the Echinoderms has the power of secreting carbonate of lime, and a more or less definite integumentary skeleton is thus usually produced. Not only is this exoskeleton in general readily preserved in the fossil state, but its minute structure is so characteristic that even the smallest fragment can usually be recognised with certainty by the help of the microscope. In the first place, the calcareous tissue of the Echinodermal exoskeleton has a very characteristic crystalline structure. "Each plate, each spine, and each joint is mineralogically and optically, as it were, made out of a single crystal of calcite, having its principal axis perpendicular to the plane of the plate, or parallel to the axis of a spine or joint, the growth from first to last being in perfect crystalline continuity" (Sorby). In recent Echinodermal skeletons, this crystalline structure is only recognisable by the optical phenomena displayed by thin sections under the microscope; but the skeleton of fossil forms, as the result of mineralisation, usually exhibits, in its minutest fragments, the unmistakable rhombohedral cleavage of calcite. In the second place, the skeleton of the Echinoderms has an equally characteristic organic structure, being made up of reticulated and anastomosing calcareous rods, which are produced by the calcification of a network of organic fibres, the uncalcified intervals of which are filled in the fresh state with living matter. All Echinodermal ossicles and plates exhibit this characteristic netted structure (fig. 236), but different forms differ in the size and disposition of the meshes; the commonest and simplest arrangement being that of parallel strata of perforated calcareous laminæ connected with one another by vertical pillars. In other cases, as in the spines of the Echinoids, the structure consists of radially-disposed, vertical, netted plates united by numerous short horizontal rods; and other types exhibit other special modifications.

In altered specimens, the minute reticulated structure of the skeleton may be largely obliterated, or even wholly unrecognisable, but the characteristic cleavage usually remains. Owing to the persistence of the characteristic micro-structure of the skeleton, even detached and otherwise indeterminable fragments of Echinoderms can commonly be recognised with certainty under the microscope, and valuable assistance is thus often afforded to the palæontologist

in his researches. Thus the singular fossils described by Eichwald under the name of *Bolboporites* can by this means be clearly determined to be of Echinodermal origin. These curious remains occur in the Ordovician rocks of Russia and Canada, and though variable in shape, have most commonly the form of inversely conical, ovoid, or clavate bodies, about a quarter of an inch or less in their long diameter, and composed of calcite with its characteristic cleavage. The narrower end of the body is usually smooth, and the sides or upper surface generally pitted with shallow depressions. Described originally as corals, the microscopic appearances of thin sections render it certain that the fossils placed under *Bolboporites* are parts

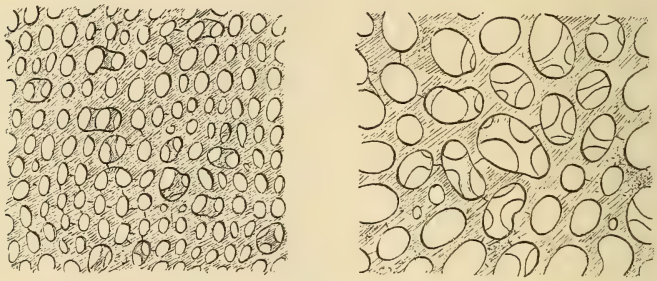

Fig. 236.—Minute structure of Echinodermal plates. A, Part of a small plate (madreporite?) of an Echinoderm from the Carboniferous rocks of Scotland, highly magnified; B, Part of an interambulacral plate of *Lepidocentrus*, from the Devonian of the Eifel, highly magnified. (Original.)

of the exoskeleton of some Echinoderm. It is difficult to speak precisely as to their nature, but they may be compared with the large tubercles or swollen spines which are developed in the integument of certain Star-fishes (*e.g.*, *Pentaceros*).

As regards their *classification*, the *Echinodermata* may be divided into seven primary groups, which are now usually regarded as classes—viz., the *Crinoidea*, *Cystoidea*, *Blastoidea*, *Ophiuroidea*, *Asteroidea*, *Echinoidea*, and *Holothuroidea*. Of these, the first is to a considerable extent extinct, and the two next are entirely so; while they exhibit certain structural peculiarities which separate them from the other classes. More particularly, the members of these three classes—viz., the Crinoids, Cystoids, and Blastoids—all possess a dorsally-developed, jointed calcareous stalk, which serves to fix them to foreign objects, and which may be only temporarily present. From the presence of this jointed stem, these three classes are grouped together in a single great division, under the name of *Pelmatozoa*. On the other hand, the Echinoids, Asteroids, Ophiuroids, and Holothuroids are devoid of this stalk at all periods of develop-

ment, and usually creep about by the aid of their tube-feet, with the oral surface of the body turned downwards. They are therefore grouped together in a common division under the name of *Echinozoa*.

As regards their *distribution*, all the recent Echinoderms are marine, and from their habit of life and their possession of a calcareous exoskeleton, the members of this sub-kingdom are largely represented as fossils, ranging from the Upper Cambrian period onwards. The classes of the *Cystoidea* and *Blastoidea* are not only extinct, but are exclusively Palæozoic; while in the *Crinoidea* we have a group which has passed its prime, and appears to be verging on extinction. On the other hand, the classes *Echinoidea*, *Asteroidea*, *Ophiuroidea*, and *Holothuroidea* appear to have attained their maximum of development at the present day. The *Asteroidea* and *Ophiuroidea* commence in the Ordovician period. The *Echinoids* commence in the Ordovician, but reach no marked development till we enter upon Mesozoic deposits. Lastly, the *Holothurians*, as might be expected from the soft nature of their integuments, are hardly known as fossils, though they seem to have existed at any rate as early as the Carboniferous period.

CHAPTER XXIII.

DIVISION A.—ECHINOZOA.

Class I. Echinoidea.

The members of this class—commonly known as Sea-urchins—are characterised by the possession of *a more or less globular, heart-shaped, discoidal or depressed body, encased in a "test" or shell, which is composed of numerous calcareous plates, in general immovably connected together. The intestine is convoluted, and there is a distinct anus. The mouth is always situated on the inferior aspect of the body, but the position of the vent varies.*

The ambulacral system of the Echinoids consists of its usual parts, and the five radial vessels given off from the circular œsophageal ring are situated within the shell of the animal. It follows from this that the tube-feet given off from the radial vessels can only reach the exterior by passing through perforations in the plates of the calcareous test. Hence the outer surface of a Sea-urchin exhibits five longitudinal areas which are "radial" in position and correspond with the five radiating ambulacral vessels, and the plates of which are more or less extensively perforated for the protrusion of the tube-feet. These so-called "ambulacral" or "poriferous" areas are separated by five zones which are "interradial" in position, have imperforate plates, and are known as the "interambulacral" areas. The external opening of the ambulacral system is closed by a spongy or porous plate—the "madreporite"—which is almost invariably situated on the apex of the test in one of the interradii. In the extinct *Echinocystites* (*Cystocidaris*) alone the madreporite is removed from its normal position, and is placed "close to the apical pole."

As regards the digestive system, the mouth is always placed on the under surface of the body, and may be central or excentric in position. The mouth is sometimes edentulous, but in other cases a complicated apparatus of calcareous teeth is developed. The anus

in many cases is placed at the summit of the test, and is surrounded by the so-called "apical disc" or "dorso-central system"; but it is in other cases marginal or submarginal, being then separated from the apical disc, and being almost always situated in the posterior interradius. In *Echinocystites* (*Cystocidaris*) alone the anus is excentric and interradial, but is placed near the apex.

The radial nerve-cords run along with the radiating ambulacral vessels in the inside of the shell, and become connected at their terminations with a series of perforated plates ("ocular plates") which form part of the so-called "apical disc," and which are "radial" in position. The generative glands occupy the "interradial" areas, and their ducts normally open by perforations in the so-called "genital plates," which likewise form part of the "apical disc."

It is necessarily principally with the test of the Echinoids and its appendages that the palæontologist is concerned, and these structures must therefore be considered in some detail. The test of the *Echinoidea* may be regarded as essentially composed of the so-called

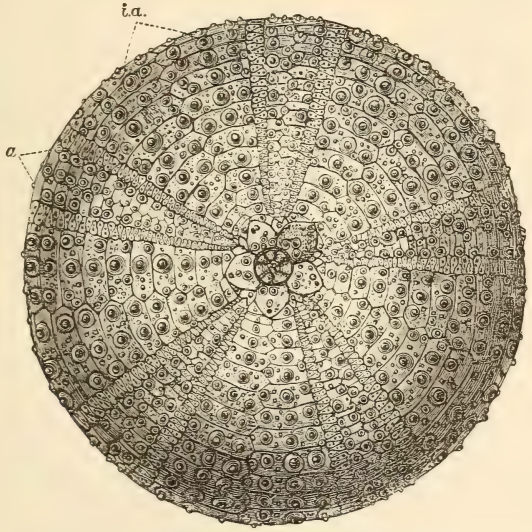

Fig. 237.—Echinoidea. Test of *Echinus esculentus*, viewed from above. *a*, One of the ambulacral areas; *ia*, One of the interambulacral areas.

"corona" and of the "apical disc"; though minor and less constant plates are likewise developed in the membranes surrounding the mouth and anus respectively.

The "corona" forms the main element of the test, and is composed of numerous calcareous plates, more or less firmly united to one another by their edges, arranged in rows, and bearing different

names according to their position and function. In the singular Urchins which constitute the family of the *Echinothuridæ*, as also in various Palæozoic Echinoids, the plates of the test overlap one another in an imbricating manner, so that the shell becomes flexible. As a rule, however, the corona forms an immovable case or box within which the animal is contained; and its growth is carried on by additions made to the edge of each individual plate by the progressive calcification of an organised membrane which passes between the "sutures," or the lines where the plates come in contact with one another. The first circle of the coronal plates is developed round the mouth, and the vertical growth of the test is carried on by the intercalation of successive rows of plates between those already formed and the apical disc.

The corona is composed of ten alternating meridional zones, of which five are radial in position and are perforated, while five are interradial and are imperforate. In all the recent Echinoids, and in all the fossil forms except the Palechinoids and the Cretaceous *Tetracidaris*, each of these ten zones is composed of two rows of plates, there being thus twenty meridional rows of plates altogether. The five interradial zones are spoken of as the "interambulacral areas," and are composed of large-sized plates, which are not perforated by any apertures (fig. 237, *ia*, and fig. 238, *a*). The five radial zones, on the other hand, are termed the "ambulacral areas" or "poriferous zones," and are composed of comparatively small plates, which are perforated by minute pores for the emission of the "tube-feet" (fig. 237, *a*, and fig. 238, *b*). As a rule, the ambulacral pores are in pairs, but in a few cases the pores are unpaired. The pores of each pair may be similar or dissimilar in shape, and in many cases they are united by transverse furrows.

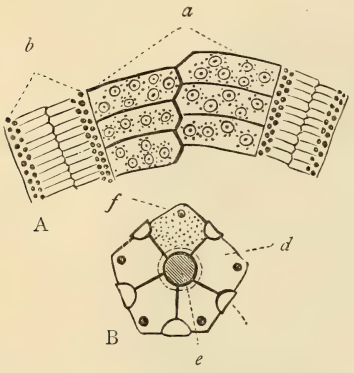

Fig. 238.—A, Portion of the test of *Holectypus hemisphericus*, enlarged, showing an interambulacral area (*a*), and an ambulacral area (*b*). B, Dorso-central system of *Hemicidaris intermedia*, enlarged: *c*, Ocular plate; *d*, Genital plate; *e*, Anal aperture; *f*, Madreporite. (After Forbes.)

In many Echinoids the ambulacral tube-feet can be protruded along the entire length of the ambulacral areas, which are perforated along their entire course from the centre of the base of the corona to the summit of the same, and which are then said to be "perfect" (*ambulacra perfecta*) or "simple" (figs. 237 and 239). In many other Echinoids, on the other hand, the ambulacral areas are not

thus continuously perforated from pole to pole, but they are "interrupted," only their upper portions being regularly poriferous.

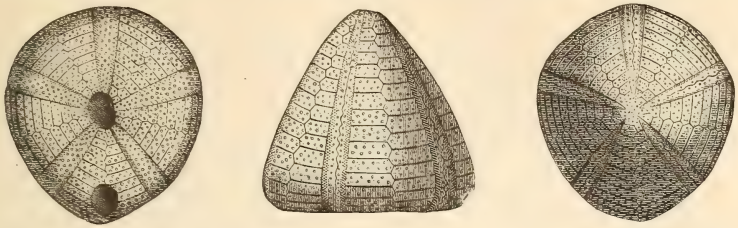

Fig. 239.—*Echinoconus conicus* (=*Galerites albogalerus*). The first figure shows the under surface with the mouth and anus; the middle figure is a side-view; and the right-hand figure shows the upper surface, with the ambulacral areas converging to the apical disc. White Chalk.

In such cases (fig. 240) the ambulacral zones are widened out superiorly, and form a kind of rosette upon the upper surface of the

Fig. 240.—*Scutella subrotunda*, showing petaloid ambulacra. Miocene.

test, when they are said to be "circumscript" (*ambulacra circumscripta*), or "petaloid."

The most important external structures of the corona are the tubercles and spines. The tubercles are rounded elevations upon

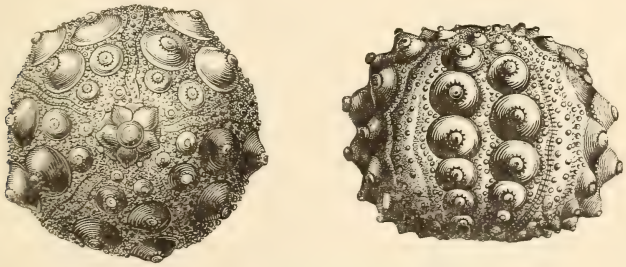

Fig. 241.—*Hemicidaris crenularis*, showing tubercles, the larger of which are perforated, and are surrounded by an areola. Jurassic.

which the spines are carried (fig. 241). They vary much in their dimensions, and receive special names, according to their size or position on the test. Ordinarily the tubercle consists of a rounded

ball or hemisphere (the "mamelon") supported upon a conical process ("the boss") which arises from the plate. The ball of the tubercle may or may not be perforated for the insertion of a ligament which is attached to the articular surface of the spine. In many cases (as in fig. 241) the base of the tubercle is surrounded by a round or oval, smooth and excavated space which is termed the "areola" or "scrobicule."

The spines are movable appendages which are jointed to the tubercles by a sort of "ball-and-socket" or "universal" joint. They are used defensively and in locomotion, and vary much in length and shape. Sometimes they are very minute; at other times they attain a length considerably exceeding the diameter of the test. Sometimes they are slender, tapering, and truly spine-like; at other times they are thickened, ovate, or almost globular (fig. 242). The spine fits on to the rounded head of the tubercle by a concave articular surface ("acetabulum"), and there may or may not be a pit at the bottom of this, for the attachment of the ligament before spoken of. Above the acetabulum or socket of the spine there is a prominent ridge or ring, more or less "milled," for the attachment of the muscular fibres which move the spine.

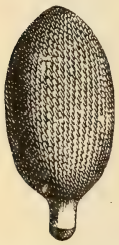

Fig. 242.—Spine of *Cidaris glandifera*. Jurassic.

At the summit of the corona in all Echinoids is found the single or double row of plates which constitutes the "apical disc" or dorso-central system, corresponding with the "calyx" of the Crinoids. In the most typical forms ("Regular" Echinoids) the plates of the apical disc surround the membrane ("periproct") in which the anus is situated (fig. 243, A); but in the so-called "Irregular" Echinoids (fig. 243, B) the apical disc simply occupies the summit of the test, and the anus is excentric, and is entirely removed from the disc. In its most ordinary condition (as in the genus *Echinus*, fig. 237), the apical disc is composed of ten plates arranged in two alternating rows of five plates each. The uppermost row consists of a cycle of five large plates of a pentagonal form, which are perforated each by the duct of a testis or ovary, and are therefore known as the "genital plates." (In the Palæozoic Echinoids from three to five pores pierce each genital plate.) One of the genital plates is larger than the others, and supports a spongy tubercle perforated by many minute apertures, like the rose of a watering-pot, and termed the "madreporite" or "madreporiform tubercle" (fig. 243, *ma*). The madreporite varies much in size, and sometimes forms almost the whole of the apical disc. The genital plates occupy the summits of the interambulacral areas, and are therefore interradial in position. Wedged in between the genital plates, and occupying the summit

of the ambulacral areas, are five smaller, heart-shaped or pentagonal plates, which are known as the "ocular plates," each of which is perforated by a minute pore lodging the rudimentary sense-organ ("ocellus") in which the radial ambulacral nerve terminates.

The anus in the Echinoids is situated in a membrane ("periproct"), which is more or less largely hardened by the development in it of small calcareous plates, which may be wholly irregular, or may form one or more regular cycles (fig. 243, *an*). As previously seen, the periproct in the "Regular" Sea-urchins is placed in the centre of the apical disc (fig. 243, A), whereas in the "Irregular" Urchins it has no connection with this structure, and is wholly

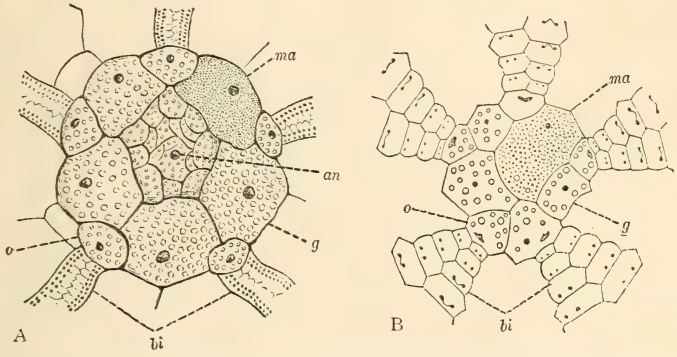

Fig. 243.—A, Apex of the shell of *Cidaris imperialis* (Recent), enlarged, after Van der Hœven; B, Apex of the shell of *Micraster* (Cretaceous), showing the condition of the apical disc in the "Irregular" Echinoids, after Zittel. *an*, Anus, surrounded by the plated "periproct"; *g*, One of the genital plates; *o*, One of the ocular plates; *ma*, Madreporite; *bi*, the two posterior ambulacral areas, constituting the "bivium."

excentric. The mouth in the Echinoids, like the anus, is situated in a coriaceous membrane ("peristomial" membrane) hardened by plates and granules of lime. Hence in macerated or fossil specimens the under surface shows, in place of the true mouth-opening, a wide vacant space ("peristome") originally occupied by the peristomial integument. The peristome may be rounded or oval, or bilabiate, or, very commonly, pentagonal, often with incisions at the angles for the accommodation of the so-called "oral gills."

The internal skeleton of the Echinoids is represented by the so-called "auriculæ" of certain types. These are calcareous arches which are ambulacral or "radial" in position, and spring from the inner surface of the lower edge of the test, just where the imperfectly calcified peristomial membrane begins. Each forms an arch over one of the radiating ambulacral vessels; and the auricles correspond, therefore, with the so-called "ambulacral ossicles" of the Star-fishes.

Though superficially conspicuously "radial" in its symmetry, the test of the Sea-urchins can nevertheless be shown, with more or less clearness, to have also a bilateral symmetry. This can be demonstrated by the position of such an unpaired organ as the "madreporite," and is more conspicuously exhibited in the "Irregular" Sea-urchins than in the "Regular" forms, though recognisable even in the latter. Thus, if the test of a Regular Sea-urchin (figs. 237 and 243) be viewed from above while held in such a position that the madreporite is placed on the side farthest from the spectator and on his right hand, it will be seen that facing the spectator is an unpaired ambulacral area ("radius"), while on the side nearest him is an unpaired interambulacral area ("interradius"). A line drawn through the centre of these two unpaired areas gives a middle line to the body, the structures on either side being for the most part symmetrically disposed. It will further be seen that three ambulacral areas (the "trivium") are directed towards the side farthest from the spectator (the "anterior" side); while two (the "bivium") are directed "posteriorly," or towards the side facing the spectator. The unpaired ambulacral area is therefore "anterior," and the unpaired interambulacrum is "posterior." In the "Irregular Sea-urchins" the bilaterality is still more marked, the unpaired anterior ambulacrum being usually different to the others in form or size; while the anus is commonly placed on the ventral side of the body, in the unpaired posterior interambulacrum.

As regards *classification*, the class of the *Echinoidea* is divided by Zittel into the two orders of the *Palechinoidea*, in which the test consists of more or fewer than twenty meridional rows of plates, and the *Euechinoidea*, in which there are constantly twenty rows of plates in the shell. The Palechinoids comprise the three groups of the *Cystocidaridæ*, *Bothriocidaridæ*, and *Perischoëchinidæ*, and the Euechinoids are divided into the two groups of the *Regulares* and *Irregulares*, according as the test is of the "regular" or "irregular" type.

As regards their distribution in time, all the Echinoids of the Palæozoic formations except *Eocidaris* belong to the order of the *Palechinoidea*, and a single member of this division (*Anaulocidaris*) is known to exist in strata of Triassic age, the division being otherwise unrepresented in Mesozoic or Tertiary deposits. The earliest types of the Palechinoids are found in the Ordovician rocks. On the other hand, the Euechinoids make their first appearance, so far as certainly known, in the Permian (*Eocidaris*), and attain a marvellous development in the Jurassic and Cretaceous periods. In the Tertiary rocks, on the contrary, the number of known fossil forms is reduced, most of the Kainozoic types being characteristic of shallow water, and many of the genera being still in existence. Upon the whole, the Euechinoids may be considered as having attained their maximum development in the period of the Chalk.

In the following condensed account of the characters and geological distribution of the chief groups of the Echinoids, the less important types are necessarily omitted. The arrangement adopted by Zittel has been followed in the main.

Order I. Palechinoidea.

This order comprises all those Urchins in which *the test is made up of more or (rarely) fewer than twenty meridional rows of plates: while the plates of the apical disc are perforated by two or more pores each, or may be in part imperforate.* As a general rule, there is an increase in the number of rows of plates forming the test of the Palechinoids, as compared with that of the Euechinoids, the interambulacral areas usually consisting of more than two rows of plates each (fig. 244). In some cases, the ambulacral as well as the interambulacral areas may consist of more than two rows of plates each, as, for example,

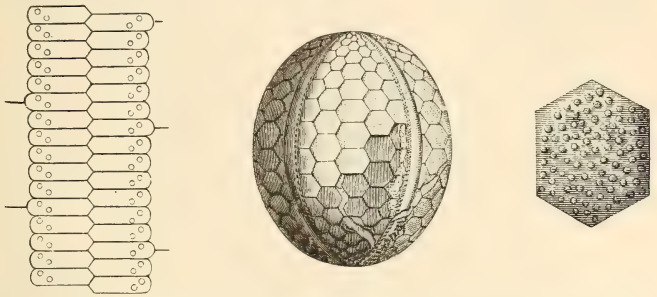

Fig. 244.—*Palæchinus ellipticus.* The left-hand figure shows a portion of an ambulacral area enlarged. The right-hand figure exhibits a single interambulacral plate.

in the genus *Melonites* (fig. 247). On the other hand, in the genus *Bothriocidaris* there is a reduction instead of a multiplication of the normal number of rows of plates in the test, the interambulacral areas consisting of one row of plates only. Furthermore, in many of the Palechinoids the test becomes more or less flexible, owing to the fact that the plates are not suturally united by their margins, but overlap by means of bevelled edges, the structure of the shell thus resembling that seen in the existing group of the *Echinothuridæ*. In all the Palechinoids there is a large peristomial aperture, and a well-developed masticatory apparatus ("Aristotle's lantern") was present. In all except *Echinocystites* (*Cystocidaris*), the test is "regular," the anus being placed at the summit of the shell and surrounded by the apical disc. The genital plates are perforated by from three to five pores each; and the ocular plates have usually two pores each, but are in other cases imperforate (fig. 244).

The order of the Palechinoids includes the three sub-orders of the *Cystocidaridæ*, *Bothriocidaridæ*, and *Perischoëchinidæ*, all of which are wholly confined to the Palæozoic period, with the exception of the last, which is represented in the Trias by the imperfectly known genus *Anaulocidaris*. It is interesting to note that this ancient

series of Echinoids possesses both "regular" and "irregular" types, and in this respect runs parallel with the later group of the Euechinoids. It is to be remembered, however, that the abnormal *Echinocystites* (*Cystocidaris*) exhibits an irregularity of structure which differs considerably from that which characterises the "Irregular" Euechinoids.

The sub-order of the *Cystocidaridæ* comprises only the aberrant genus *Echinocystites* (=*Cystocidaris*, Zittel), in which the interambu-

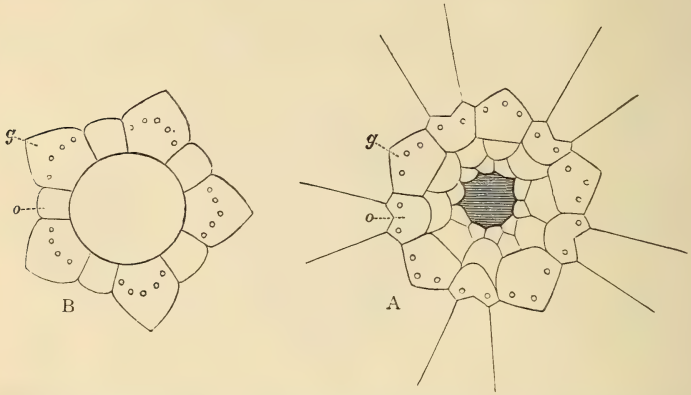

Fig. 245. — A, Apical disc of *Palæchinus*, enlarged (after Baily); B, Apical disc of *Melonites* (after Meek and Worthen): *g*, One of the genital plates; *o*, One of the ocular plates.

lacral zones are composed each of several rows of plates, and the anus is excentric. The two known species of the genus are found in the Silurian rocks of Britain.

The test in *Echinocystites* is spheroidal or ovoid, with narrow ambulacral and broad interambulacral areas, the latter being formed by several irregular rows of imbricated calcareous plates, carrying spines. The mouth is on the under surface, central in position, with a well-developed masticatory apparatus; while the anus is excentric, but has the unique position of being not widely remote from the apex in one of the interambulacral spaces. The madreporite is also quite peculiar in not being at the apex of the shell, but in being placed excentrically in one of the interambulacra. Another remarkable point is that the anus is closed by a valvular pyramid of calcareous plates, a feature highly characteristic of the Cystideans.

The sub-order of the *Bothriocidaridæ* includes the single genus *Bothriocidaris*, in which the interambulacral areas are composed each of a single row of plates, and the anus is placed in the centre of the apical disc. The two known species of the genus have been found in the Ordovician rocks of Russia (Esthonia).

The test in *Bothriocidaris* is spheroidal and "regular," the anus being situated in the centre of the apical disc, and the ambulacra being "perfect." The plates of the test are immovably connected, and the interambulacral zones are composed of a single row of plates only, while the ambulacral zones have two rows each (fig. 246, *a*). There are thus fifteen meridional rows of plates in the test in all. The peristomial

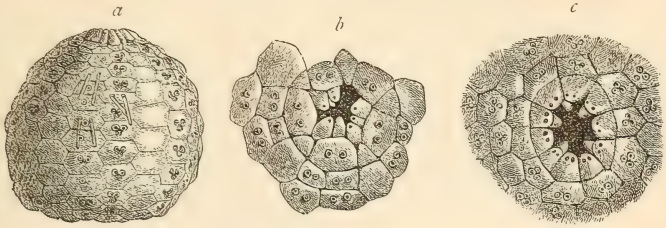

Fig. 246.—*Bothriocidaris Pahleni*, Ordovician. *a*, The test viewed sideways, of the natural size; *b*, The apical disc and anus, enlarged; *c*, The mouth, enlarged. (Copied from Zittel, after Fr. Schmidt.)

membrane (fig. 246, *c*) is furnished with triangular valvular plates surrounding the mouth-opening, and similar plates encircle the aperture of the anus (*b*).

The sub-order of the *Perischoëchinidæ* comprises all the known remaining types of the Palechinoids, and is characterised by the fact that the test is composed of more than twenty meridional rows of plates, and is "regular" in type, the anus being situated in the centre of the apical disc. The interambulacral areas always possess more than two rows of plates each, and the ambulacral areas likewise may consist of more than two rows each (as in *Melonites* and *Oligoporus*, fig. 247). The mouth is placed in the centre of the lower surface, and is furnished with a masticatory apparatus, while the anus is situated at the summit of the test. The genital plates have from two to five pores, and the ocular plates may have two pores each or may be imperforate (fig. 245). Very commonly the test becomes more or less flexible in consequence of the imbrication of its component plates, the edges of which are often bevelled. All the *Perischoëchinidæ* are Palæozoic, with the exception of the Triassic genus *Anaulocidaris*. The earliest types are found in the Silurian, but the group attains its maximum in the Carboniferous rocks.

Of the genera of the *Perischoëchinidæ*, *Palæchinus* possesses a spheroidal test (fig. 244), the plates of which abut against one another without any overlapping. The ambulacral areas are comparatively narrow, of two rows only, each plate perforated by two pores. The interambulacral areas are broad, and are composed of from four to eight rows of plates. The apical disc (fig. 245, A) has five triply perforated genital plates, and an equal number of doubly perforated ocular plates (Baily), but the latter are wanting in *P. sphæricus*. A single species of

the genus occurs in the Silurian rocks, but a number of forms are found in the Carboniferous Limestone.

In the genera *Melonites* and *Oligoporus*, of the Carboniferous rocks, we have large spherical Urchins, in which the test appears to have been rigid, though some of the plates are occasionally bevelled off, so as to articulate in an overlapping manner with one another. In *Melonites* (fig. 247) there is a multiplication of the plates of both the interambulacral and ambulacral areas, the former consisting in the middle of seven or eight rows, while the latter are of eight or ten rows, or, in a British species, of from twelve to fourteen rows. The central two rows of ambulacral plates are larger than the rest and elevated above them, and each plate of these areas is doubly perforated. The apical disc (fig. 245, B) is composed of

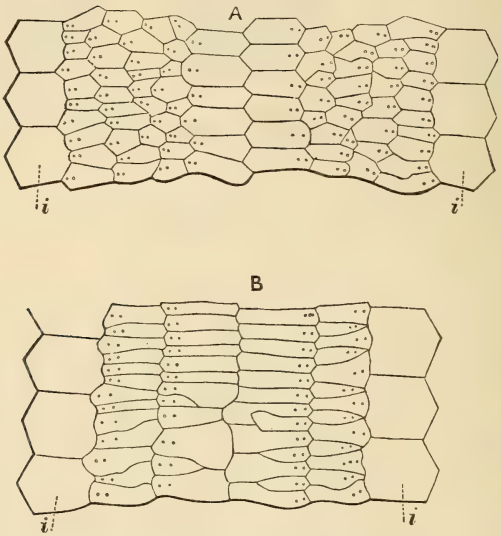

Fig. 247.—A, Portion of an ambulacral area of *Melonites multiporus*. B, Portion of an ambulacral area of *Oligoporus Danæ*: *i*, Lateral row of interambulacral plates. Carboniferous. (Meek and Worthen.)

the normal ten plates, but the ocular plates are sometimes imperforate, and the genital plates are furnished with from three to five pores.

Oligoporus (fig. 247, B) is very similar to *Melonites*, but the ambulacral areas consist each of only four rows of plates.

Allied to *Melonites* is the Carboniferous genus *Lepidesthes*, in which the ambulacra are composed of no less than ten rows of plates, the interambulacra being comparatively narrow and composed of six or seven rows of plates. The plates of the test, as in various other Palechinoids, are imbricated, the test thus becoming flexible, as it is in the recent genus *Asthenosoma*. The imbrication in the flexible Palechinoids differs from that of the *Echinothuridæ* in the fact that the overlapping of the interambulacral plates is from below upwards, and that of the ambulacral plates from above downwards, the reverse of this taking place in *Asthenosoma* and its allies.

A well-known Carboniferous genus is *Archæocidaris* (fig. 248), in which

the test is spheroidal, the ambulacra are only two-rowed, and the interambulacra are wide and are composed of three or more rows of plates. The interambulacral plates (fig. 248, *b*) carry each a large perforated tubercle, surrounded by a ring, supporting a long echinulate spine (*d*). As shown by Mr John Young, the test must have possessed a certain degree of flexibility, as the edges of some of the interambulacral plates are bevelled off. The Devonian and Carboniferous genus *Lepidechinus*

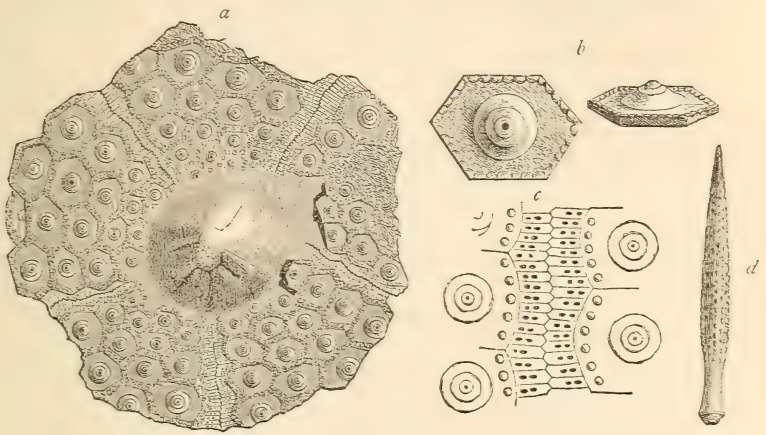

Fig. 248.—*Archæocidaris Wortheni*, from the Carboniferous Limestone of North America. *a*, Fragment of the under side, with the teeth, of the natural size; *b*, An interambulacral plate, viewed from above and sideways, showing the hexagonal form, and the spine-bearing tubercle; *c*, Portion of an ambulacrum, enlarged: *d*, One of the spines, of the natural size. (Copied from Zittel—after Hall.)

differs from the preceding in the fact that the plates of the test are strongly imbricated, the shell thus becoming quite flexible. The ambulacral areas are two-rowed, but the interambulacra have from nine to eleven rows of plates.

Differing in some respects from the preceding are the genera *Perischodomus*, *Rhoëchinus*, and *Lepidocentrus*, of which the two first are Carboniferous, while the last is found in the Devonian rocks. In all these genera, the test is rendered flexible by the overlapping of the interambulacral plates.

Lastly, the Triassic genus *Anaulocidaris*, known by detached plates and spines, is allied to *Archæocidaris*, and, so far as known, is the latest representative of the division of the Palechinoids.

Order II. Euechinoidea.

This division comprises all those Sea-urchins in which *both the ambulacral and interambulacral areas are constantly two-rowed, the test thus consisting of twenty rows of plates. The genital and ocular plates are almost always perforated by a single opening each; and a masticatory apparatus may be present or absent. The test may be "regular" or "irregular."*

The order of the Euechinoids includes all the normal Sea-urchins, and the distribution of the group in time is remarkable. No Euechinoid has hitherto been detected in any Palæozoic deposit anterior to the Permian, but a vast development of the forms of this division takes place in rocks of Mesozoic age, while all the Tertiary and Recent Urchins also belong to this group. In the Jurassic and Cretaceous rocks the Euechinoids attain their maximum development, and very numerous forms are also known from the Tertiary formations.

The *Euechinoidea* may be divided into the two sub-orders of the *Regulares* and *Irregulares*, the characters and chief groups of which will be briefly treated of in the following pages.

Regular Euechinoids.

The sub-order *Regulares* (*Echinoidea endocyclica*) includes all those Euechinoids in which the test is "regular," the mouth being inferior and central, while the anus occupies the centre of the superior surface, and is surrounded by the apical disc. The form of the test is usually spheroidal, and the ambulacral areas are perfect, and are all alike. The mouth is furnished with a masticatory apparatus. In *Tetracidaris* the interambulacra are in part four-rowed, but in all others they are two-rowed, as are the ambulacra in all cases. The members of this sub-order appear to be the most ancient forms of the Euechinoids, being tolerably well represented in the Trias, and even occurring in the still older Permian formation (*Eocidaris.*) They are largely represented in the Jurassic and Cretaceous formations, but begin to diminish in numbers in the Eocene Tertiary. The *Regulares* may be divided into the four principal families of the *Cidaridæ*, *Salenidæ*, *Echinothuridæ*, and *Glyphostomata*, the more important forms of which are noticed below.

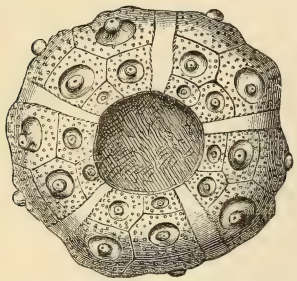

Fig. 249.—Under surface of the test of *Cidaris vesiculosa*, of the natural size. Chalk. (After Wright.)

Family 1. *Cidaridæ.*—In this family the test is spheroidal, and more or less flattened at the oral and anal poles. The ambulacral areas (fig. 249), are very narrow, often flexuous, and never provided with large tubercles. The interambulacral areas are wide, and carry large perforated tubercles, surrounded by an areola, and supporting the primary spines. The spines are of two sizes, the primary ones usually more or less cylindrical, clavate, or fusiform, and generally longitudinally ridged or tuberculate (fig. 242).

Of the genera of this family, *Cidaris* itself (fig. 249) is the most important, ranging from the Trias to the present day. *Rhabdocidaris* is Jurassic and Cretaceous; *Diplocidaris* is Jurassic; and the *Porocidaris* of the Secondary and Tertiary periods has now been detected by Sir Wyville Thomson in a living condition. In the aberrant Cretaceous genus *Tetracidaris*, the interambulacral zones are composed each of four rows of plates, reduced to two rows in the neighbourhood of the apex.

The genus *Eocidaris*, based upon a form which occurs in the Permian rocks of Germany, has been generally placed among the Palechinoids, in the vicinity of *Archæocidaris*. According to the recent researches of Kolesch, however, the interambulacral and ambulacral areas in *E. Keyserlingi* are two-rowed, and the genus is therefore properly referable to the Euechinoids. The Devonian and Carboniferous Urchins which have been referred to *Eocidaris* have more than twenty rows of plates in the corona, and must therefore be removed from this genus as now understood. With our present knowledge, therefore, the Permian *Eocidaris* must be regarded as the oldest type of the Euechinoids.

Family 2. *Salenidæ*.—In this family the test is generally spheroidal, hemispherical, or depressed, and the ambulacral areas are always narrow, sometimes straight, sometimes flexuous, and without large primary tubercles. The interambulacral areas are always provided with two rows of large tubercles, with crenulated bosses, which may or may not be perforated. The leading character of the family, however, is to be found in the apical disc (figs. 250 and 251), which is of unusually large size, and possesses a supernumerary or "suranal" plate in addition to the ten normal plates. This suranal plate (fig. 250, *s*) is placed in front of the anus, and it may be single, or it may be represented by several (not more than eight) elements. From a morphological point of view the suranal plate may be compared with the "dorso-central" plate of the Crinoids, while the genital and ocular plates respectively correspond to the basals and radials of the Crinoidal calyx. The "madreporite" is imperfectly developed, and often hardly recognisable. The peristomial membrane is furnished with calcareous plates which differ from the peristomial plates of the *Cidaridæ* in the fact that the rows of ambulacral pores are not continued over them to the mouth.

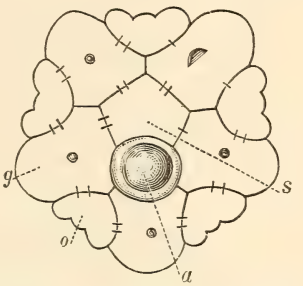

Fig. 250. — Apical disc of *Peltastes Wrightii*, one of the *Salenidæ*. *a*, Anus; *g*, One of the genital plates; *o*, One of the ocular plates; *s*, Suranal plate. Twice the natural size. Cretaceous (Lower Greensand). (After Wright.)

The genus *Salenia* itself (fig. 251) appears for the first time in the Cretaceous rocks, and still survives at the present day. *Peltastes*, with a similar range in time to *Salenia*, differs from the latter in the fact that

the anus is placed in the middle line; and the *Goniophorus* of the Chalk is a closely allied form. *Acrosalenia*, again, ranges from the Lias to the Chalk.

Family 3. *Echinothuridæ*.—In this small but highly remarkable division of the *Echinoidea* the test is "regular," the anus being

Fig. 251.—*Salenia personata*. The left-hand figure represents the upper surface of the shell, and shows the anus surrounded by the apical disc. The right-hand figure shows the under side with the peristomial space.

placed in the centre of the apical disc, and the ambulacral areas being continuous; but the plates of both the ambulacral and interambulacral areas are imbricated and overlap one another (fig. 252), the test thus becoming flexible. In this abnormal character, the *Echinothuridæ* agree with some of the Palæozoic Urchins, but they

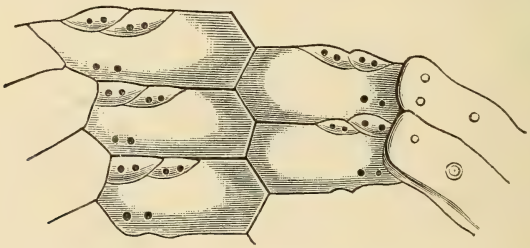

Fig. 252.—Portion of one of the ambulacral areas of *Echinothuria floris*, enlarged four times. Chalk. (After Wright.)

differ from these, and agree with the ordinary Regular Echinoids in having the test composed of no more than twenty rows of plates.

The only fossil forms of this group, as yet discovered, are referable to the Cretaceous genus *Echinothuria*, the true affinities of which have now been elucidated by the discovery of the extraordinary living types referred to the genera *Asthenosoma* and *Phormosoma*.

Family 4. *Glyphostomata*.—In this family the ambulacral areas are not much narrower than the interambulacral, and both as a rule carry primary tubercles. The peristomial membrane usually carries irregular calcareous ossicles, but is not completely plated, and the peristome is furnished with more or less marked incisions at its angles. "Auriculæ" are present. This family is divisible into the

two minor groups of the *Diadematidæ* and the *Echinidæ*, both of which appear in the Secondary period, and are represented at the present day.

In the *Diadematidæ*, the pairs of ambulacral pores (fig 253) form a single row on each side of the ambulacral areas, except near the apex and the peristome, where more than one row of pore-pairs may be developed. The test is generally circular or pentagonal,

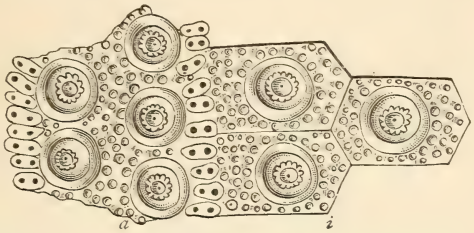

Fig. 253.—Portion of the test of *Pseudodiadema Fittonii*, enlarged four times. *a*, Ambulacral area; *i*, Interambulacral area. Lower Greensand (Cretaceous). (After Wright.)

more or less depressed and flat below. The ambulacral areas are wide, and carry two rows of large primary tubercles, equal in size to the two or more rows of tubercles upon the interambulacra. The tubercles are sometimes perforated, sometimes imperforate, and they may or may not be crenulated. The spines are cylindrical and slender, and usually of considerable length. In the living *Diadema* the spines are long, tubular, and covered with imbricated scales

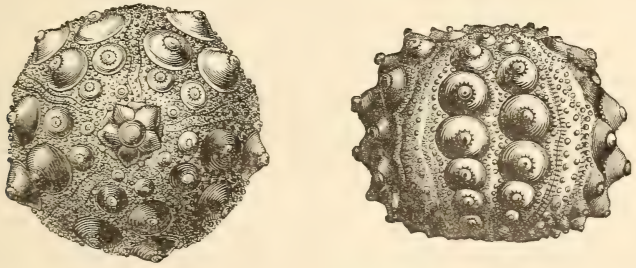

Fig. 254.—*Hemicidaris crenularis*, showing tubercles, the larger of which are perforated, and are surrounded by an areola. Jurassic.

arranged in oblique rings. The *Diadematidæ* are very extensively represented in the Secondary rocks, the earliest forms appearing in the Upper Trias; the Tertiary forms are less numerous, and a limited number of types referable to the group still exist.

Of the genera of this family, *Hemicidaris* (fig. 254) has a spheroidal, more or less depressed test, with a general resemblance to that of the

Cidaridæ. The ambulacral areas, however, though narrow and mostly undulated, are wider than in the *Cidaridæ*, and are provided with comparatively large tubercles, which may be developed inferiorly only (*Hemicidaris*), or which may extend along the entire length of the area (*Acrocidaris*). The interambulacral areas are wide, and carry very large perforated tubercles with crenulated bosses. The spines are usually long, cylindrical, and tapering. The type-genus of this family is *Hemicidaris* (fig. 254), which ranges from the Upper Trias to the Lower Cretaceous inclusive. In *Acrocidaris*, of the Jurassic and Cretaceous periods, the ambulacral areas are comparatively wide. In the genus *Pseudodiadema*, which ranges from the Lias to the Eocene Tertiary, the spines are solid and microscopically striated, and the tubercles are perforated (fig. 253). On the other hand, in the genus *Cyphosoma* and in a number of allied forms, the tubercles are imperforate. The species of *Cyphosoma* are mostly found in the Chalk, but some occur in the Eocene, and a single species survives at present. *Hemipedina*, again, which begins in the Jurassic rocks, and which is also represented at the present day by a single living species, is like *Pseudodiadema*, but the tubercles are not crenulated. This is also the case with the extensive genus *Goniopygus* (fig. 255), which is principally Cretaceous in its range, though also occur-

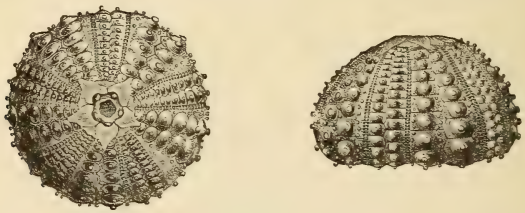

Fig. 255.—*Goniopygus major*, viewed from above and sideways, of the natural size. Cretaceous.

ring in the Eocene rocks. In the great size of the apical disc this genus reminds us of *Salenia*, but it wants the supernumerary "suranal" plate of the latter. Among the many other genera of this sub-family, *Cottaldia* (Chalk to Recent), *Glypticus* (Jurassic), *Codiopsis* (Cretaceous), and *Temnechinus* (Pliocene) may be specially mentioned; but the number of types included in this group is too large to permit of further particularisation.

In the sub-family of the *Echinidæ*, the general structure of the test is much the same as in the *Diadematidæ*, but the ambulacral plates consist of at least three "pore-plates" fused together, and the pairs of ambulacral pores are arranged in three or more rows (rarely in two rows only) on each side of each ambulacrum (fig. 256, *b*). The test is usually globular or hemispherical, and the ambulacral areas are comparatively wide, and carry two or more rows of tubercles. The interambulacral areas are wide, and carry primary tubercles, which are always imperforate, and are never of very large size. The spines are short and awl-shaped, and their surface is marked with fine longitudinal lines.

In many genera of the *Echinidæ* each ambulacral plate carries three pairs of pores, and types exhibiting this character appear as early as the Jurassic period. One of the leading genera thus characterised is *Stomechinus* (fig. 256), which is found in both the Jurassic and Cretaceous deposits. An allied Jurassic genus is *Polycyphus;* while *Salmacis* and *Echinus* proper begin in the Eocene Tertiary, and are represented at the present day by living species. On the other hand, in other genera of the *Echinidæ* each ambulacral plate carries more than three pairs of ambulacral pores. The forms of this group are comparatively modern, a few

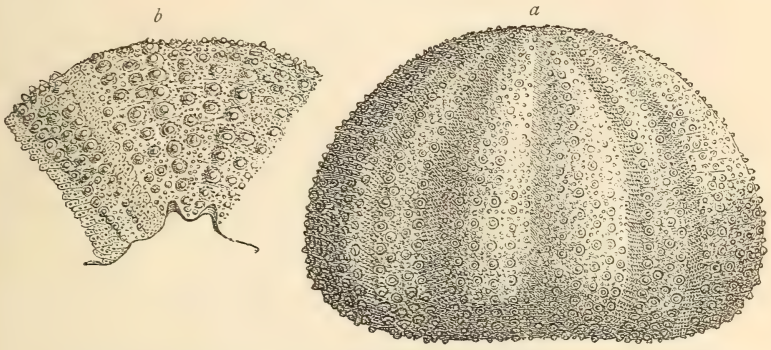

Fig. 256.—*Stomechinus lineatus*, from the Jurassic rocks (Coral Rag) of Germany. *a*, A specimen viewed in profile, of the natural size; *b*, Part of the oral region of the same. (After Zittel.)

types (*Phymechinus*, *Pedinopsis*, &c.) occurring in the Upper Jurassic or Cretaceous rocks, but the majority being Tertiary or Recent. The two most important members of this section are *Sphærechinus* and *Strongylocentrotus*, both of which begin in the Pliocene Tertiary, and are represented by living species.

Irregular Euechinoids.

The sub-order of the *Irregulares* (*Echinoidea exocyclica*) includes all those Euechinoids in which the test is "irregular," the anus being excentric, and not connected with the genital disc. The mouth is placed on the lower surface, and may be central or excentric in position, while a masticatory apparatus may or may not be present. The test is bilaterally symmetrical, commonly of an oblong, pentagonal, heart-shaped, or discoidal figure (as in the common "Heart-urchins" and "Cake-urchins"). There are commonly only four genital plates in the apical disc, and the ambulacra may be either simple or petaloid.

The Irregular Euechinoids have been divided into two groups, according as they possess a masticatory apparatus (*Gnathostomata*), or are without teeth (*Atelostomata*); but these two groups are very closely connected, and it seems that too much weight has been

attached to the value in classification of this particular character. Moreover, it has not in all cases been certainly ascertained whether or not a masticatory apparatus is actually present. Here, therefore, it will be sufficient to divide the Irregular Euechinoids into the six families of the *Conoclypeidæ*, *Clypeastridæ*, *Echinoconidæ*, *Cassidulidæ*, *Holasteridæ*, and *Spatangidæ*. The oldest types of the whole series (*Pygaster* and *Galeropygus*) appear in the Lias, and numerous forms are known in the later Mesozoic and Tertiary deposits, while the group is largely represented at the present day.

Family 1. *Conoclypeidæ*.—The Urchins of this family have a rounded or ovoid, gibbous test, covered with small tubercles and spines. The ambulacra are petaloid, but are continued inferiorly as far as the mouth. There are only four genital plates, and the madreporite is of large size. The mouth is placed in the centre of the inferior surface, and the anus is submarginal. Teeth are present, and "auricles" are also developed. All the members of this family

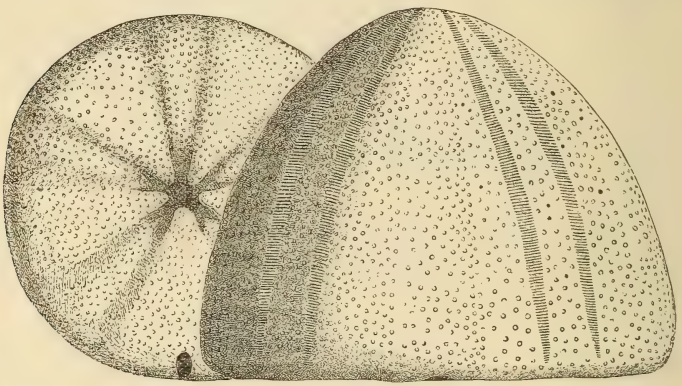

Fig. 257.—*Conoclypus conoideus*, from the Eocene rocks of Germany, viewed sideways and from below, reduced in size. (After Zittel.)

except one are referable to the single genus *Conoclypus* (fig. 257), the species of which range from the Chalk to the present day, being most abundant in the Eocene Tertiary.

Family 2. *Clypeastridæ*.—In this family the test is usually circular or elliptical, generally depressed, the surface covered with small tubercles surrounded by sunken, ring-like *areolæ*, and carrying hair-like spines. The dorsal portions of the ambulacral zones are wide and petaloid, and the ambulacral pores are confined to the apical "rosette" thus formed. The mouth is inferior, central, and armed with teeth; and the anus is marginal or infra-marginal. The madreporite occupies almost the whole of the apical disc, and the genital plates (four or five in number) are only indicated by their pores.

The interior of the shell, as a rule, is more or less subdivided by calcareous pillars or septa. The Clypeastrids range from the Chalk to the present day, but the early forms of the group are small.

The typical Clypeastrids have the test more or less gibbous superiorly, the two most important genera being *Echinocyamus* and *Clypeaster*. The first of these includes small oval Urchins, which range from the Chalk to the present day; while the latter (fig. 258) comprises large, massive, elliptical or pentagonal types, with a conspicuously developed ambulacral rosette.

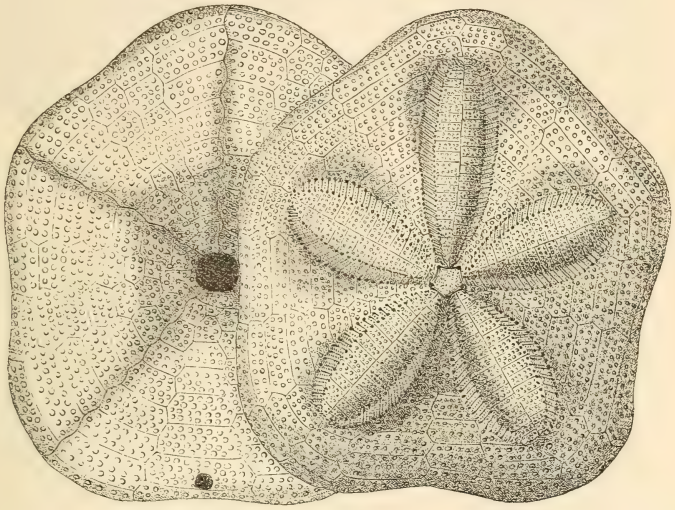

Fig. 258.—*Clypeaster grandiflorus*, from the Miocene Tertiary, viewed from above and below, slightly reduced in size. (Copied from Zittel, after Desor.)

The oldest known species of *Clypeaster* appear in the Eocene Tertiary, but there are numerous Miocene and Pliocene forms, and the genus is well represented in recent seas.

In another group of Clypeastrids, exemplified by such genera as *Scutella* and *Echinarachnius*, the test is so flattened as to become discoid or cake-like. The genus *Scutella* (fig. 240) is wholly confined to the Eocene and Miocene deposits, while the closely allied types placed under *Echinarachnius* are still represented in existing seas.

Family 3. *Echinoconidæ*.—In this family the test is usually circular or subpentagonal, the ambulacral areas being narrow, and running continuously from the apical disc to the peristome (fig. 259). Both the ambulacral and interambulacral areas carry small, crenulated, and perforated tubercles, which support short and awl-shaped spines. The mouth is inferior and central, and the excentric anus may be superior in position, but is usually inferior or marginal. There may be only four genital plates in the apical disc.

The position of the family *Echinoconidæ* has been rendered doubtful by the researches of Professor Martin Duncan, who has shown that the type-genus, *Echinoconus*, usually regarded as possessing teeth and "auricles," is really destitute of both these structures. In accordance with this, Dr Duncan would remove the genus *Echinoconus* to the family of the *Cassidulidæ*. The forms included in the family

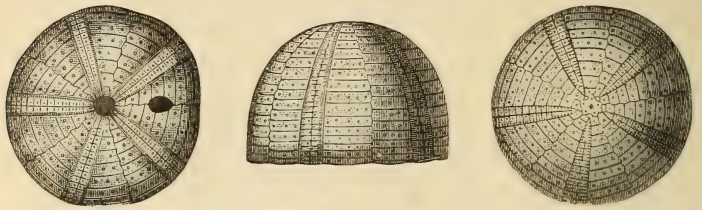

Fig. 259.—*Discoidea cylindrica*. The right-hand figure shows the summit of the shell, with the genital disc. The left-hand figure shows the base of the shell, on which are situated both the mouth and anus. Cretaceous.

Echinoconidæ are almost wholly confined to the Jurassic and Cretaceous rocks, so far as at present known; but a living species of *Pygaster* has been detected, and this genus, at any rate, must have representatives in the Tertiary rocks.

The genus *Echinoconus* (=*Galerites*) is exclusively confined to the Cretaceous rocks, *E. vulgaris* and *E. conicus* (=*Galerites albogalerus*) being very common species in the White Chalk. The test in this genus (fig. 239) is rounded or subpentagonal, often conical, with a nearly flat base. The anus is infra-marginal or nearly marginal. *Discoidea* (fig. 259) is also confined to the Cretaceous rocks, and is nearly related to the preceding, but the margins of the interambulacral areas in the interior of the test are strengthened by longitudinal thickenings or ribs. *Holectypus*, again, is closely allied to *Discoidea*, but the test is depressed (fig. 260), and there are no internal ribs. The species of this genus are Jurassic and Cretaceous. Lastly, in the genus *Pygaster* (fig. 261), the anal aperture is of great size, oblong or pyriform in shape, and situated on the superior aspect of the shell. All the five genital plates are present, and are perforated for the generative ducts. The species of this genus are mostly Jurassic and Cretaceous, but a recent species is known to exist.

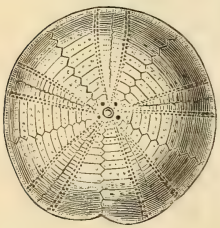

Fig. 260.—Test of *Holectypus hemisphericus*, viewed from above—Jurassic. (After Edward Forbes.)

Family 4. *Cassidulidæ*.—This family comprises irregular Urchins in which the mouth is invariably edentulous, and is placed centrally or subcentrally on the inferior surface, while the anus is excentric, and is generally placed on the upper surface (fig. 262). The test is generally oval or elliptical, and the ambulacral zones are approxi-

mately similar, and may be either simple (*Echinonidæ*) or petaloid (*Echinolampadæ*). Only four genital plates are furnished with per-

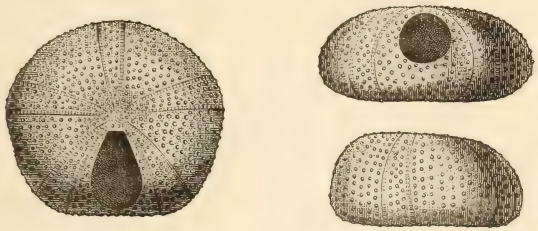

Fig. 261.—*Pygaster truncatus*, viewed from above, from behind, and from one side. Cretaceous.

forations for the generative ducts. The range of the family is from the Jurassic to the present day inclusive.

In one series of the *Cassidulidæ*—sometimes spoken of as the *Echinonidæ*—the ambulacra are simple and linear, and the mouth is central or

Fig. 262.—*Hyboclypus gibberulus*, viewed from above, from one side, and from below. Jurassic.

subcentral. A good example of this is the Jurassic genus *Hyboclypus* (fig. 262), in which the mouth is removed towards the anterior side, the anus is in a longitudinal dorsal valley, and the apical disc is elongated, so that the posterior two ambulacra become disjoined from the anterior three. Other examples of this group are the Cretaceous and Eocene genus *Pyrina*, and the Miocene and Recent genus *Echinoneus*. In another group of the *Cassidulidæ*—sometimes spoken of as the *Echinolampadæ*—the ambulacra are petaloid, and are generally sunk in the vicinity of the mouth in grooves separated by the swollen interambulacra, giving rise to a peristomial rosette or "floscelle." Some of the members of this group make a near approach to the preceding, being without a conspicuous oral rosette, and having ambulacra of a but very slightly petaloidal form; and these have sometimes been separated to form a distinct group (*Echinobrissidæ*). Of the many forms

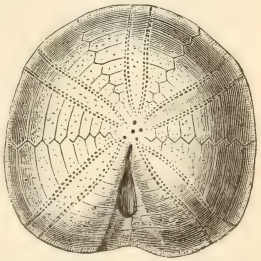

Fig. 263.—*Echinobrissus clunicularis*, Jurassic, viewed from above. (After Wright.)

included in this group the genus *Echinobrissus* is one of the most widely distributed, species of the genus being very abundant in the Jurassic rocks, but extending also into the Cretaceous. In this genus (fig. 263), the test is concave below, and the anus is placed in a dorsal sulcus. Other well-known genera are *Nucleolites* (Chalk to Recent), *Pygurus* (Jurassic and Cretaceous), *Clypeus* (Jurassic), *Pygaulus* (Cretaceous), *Cassidulus* (Cretaceous and Tertiary), *Echinanthus* (Cretaceous and Tertiary), and the Tertiary and Recent *Catopygus* and *Echinolampas*.

Family 5. *Holasteridæ*.—This family comprises ovoid Urchins, with simple ambulacra, and a generally very gibbous test. The apical disc is usually drawn out in an antero-posterior direction, the elongation being sometimes so great that the two posterior ambulacra

Fig. 264.—*Collyrites* (*Dysaster*) *Eudesi*, viewed from above, from one side, and from below. Jurassic.

are widely separated from the three anterior ones on the summit of the shell (fig. 264). The peristome is excentric, generally oblique or bilabiate; and the anus is inframarginal or marginal. The members of this family are mostly Jurassic and Cretaceous, but a number of recent forms are known to exist.

In one group of this family (the *Collyritidæ* of D'Orbigny, or the *Dysasteridæ* of other writers), the apical disc is greatly elongated, and the narrow ambulacral areas thus become more or less "disjunct," the two hinder ambulacra meeting superiorly at one end of the disc, while the three anterior ambulacra meet at the other end of the same. The principal genus of this group is *Collyrites* itself (figs. 264 and 265), in which the test is oval or somewhat heart-shaped, the mouth being inferior and excentric, and the anus being supramarginal. The elements of the apical disc are detached from one another, the anterior portion containing four perforated genital plates and three ocular plates, while the posterior portion, connected with the preceding by a narrow series of supernumerary plates, contains the two other ocular plates. The genus is represented by numerous species in the Jurassic and Cretaceous rocks. Closely allied to the preceding, and with a similar geological range, is the genus *Dysaster*.

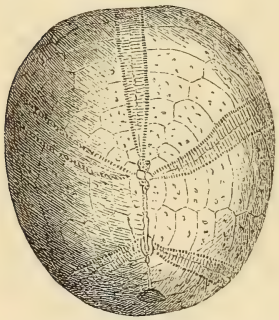

Fig. 265.—Upper surface of the test of *Collyrites elliptica*, showing long apical disc and disjunct ambulacra. Jurassic. (After Zittel.)

In another series of the *Holasteridæ*—sometimes spoken of as the *Ananchytidæ* or *Echinocoridæ*—the apical disc may be either elongated or compact, but in either case the five ambulacra all meet in it. The chief genus of this group is *Ananchytes* (fig. 266) itself, in which the test is ovate, and highly convex above, the peristome is advanced forwards and is two-lipped, and the anus is inframarginal. The species of this genus are confined to the Chalk, the commonest form being the well-known and highly variable *A. ovata*. The genus *Holaster* is nearly related to *Ananchytes*, but the test is sub-cordate, the apical disc is more elongated, and the anus is marginal or supramarginal. The species are chiefly Cretaceous, but are found in the Tertiary deposits in Australia. In *Cardiaster*, again, which is also Cretaceous, there is the additional character of the existence of a "fasciole," which passes beneath the anus and is continued on the sides of the test. As will be seen immediately, the presence of "fascioles"—that is to say, of circumscribed bands of microscopic granules, occupying definite areas and positions on the test—is highly characteristic of the *Spatangidæ*, towards which *Cardiaster* thus makes an approach.

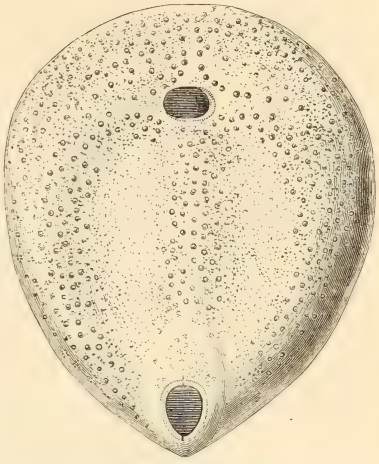

Fig. 266.—Under surface of the test of *Ananchytes ovata*, showing the position of the mouth and anus. Jurassic. (After Forbes.)

Family 6. *Spatangidæ*.—In the members of this family—often spoken of as "Heart-urchins"—the test is markedly bilateral, and is usually conspicuously heart-shaped (fig. 267). The mouth is advanced far forwards on the under side, and the anus is supra-marginal, and is placed in the posterior interambulacrum. The ambulacra are petaloid, and the unpaired anterior ambulacrum always differs more or less from the others, being usually lodged in a groove or "sulcus" (fig. 267). The mouth is typically bilabiate, but is in some cases five-sided;

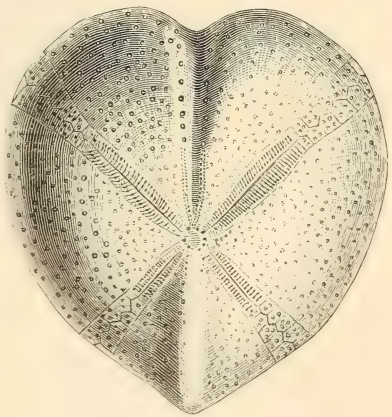

Fig. 267.—Upper surface of *Micraster coranguinum*. Cretaceous. (After Forbes.)

and, as in the preceding two families, teeth are invariably wanting. The tubercles of the test are mostly small, and carry hair-like spines; but there are larger, crenulated, and perforated tubercles for the support of larger spines. As a rule, bands of microscopic tubercles known as "fascioles" (fig. 268) are present, and occupy different positions in different genera. Sometimes the "fasciole" surrounds the ambulacral rosette, when it is said to be "peripetalous"; sometimes it is "internal," surrounding the unpaired ambulacrum; sometimes it surrounds the sides, and is said to be "lateral"; at other times it runs round the test, and is termed "marginal"; and, lastly, it may be limited to the base of the anal aperture, when it is termed "sub-anal."

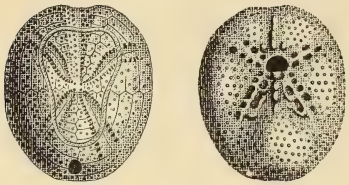

Fig. 268.—*Gualteria Orbignyana*, viewed both from above and below. The left-hand figure shows the "fasciole" cutting the ambulacral rosette. Eocene.

Of the genera of *Spatangidæ* characterised by a pentagonal mouth, the chief is *Toxaster*, the species of which are wholly Cretaceous. Of the more normal Heart-urchins, with a bilabiate mouth, *Micraster* (fig. 267) possesses a sub-anal fasciole, and is widely distributed in the Chalk, the genus being also represented in the Tertiary rocks of Australia. *Epiaster*, likewise found in the Chalk, has no sub-anal fasciole, but is otherwise similar to *Micraster*. *Hemiaster*, very abundant in the Cretaceous period, but also represented by Tertiary and living species, has a peripetalous fasciole. *Linthia* (*Periaster*) has both a peripetalous and a lateral fasciole, and ranges from the Chalk to the present day. *Gualteria* and *Macropneustes* are Eocene types; while *Schizaster*, *Brissus*, *Brissopsis*, *Echinospatagus* (*Amphidetus*), *Eupatagus*, and *Spatangus* are well-known Tertiary and Recent genera.

CHAPTER XXIV.

ASTEROIDEA, OPHIUROIDEA, AND HOLOTHUROIDEA.

Class II. Asteroidea.

The class *Asteroidea* comprises the ordinary Star-fishes, and is defined by the following characters: *The body* (fig. 269) *is star-shaped or pentagonal, and consists of a central body or "disc" sur-*

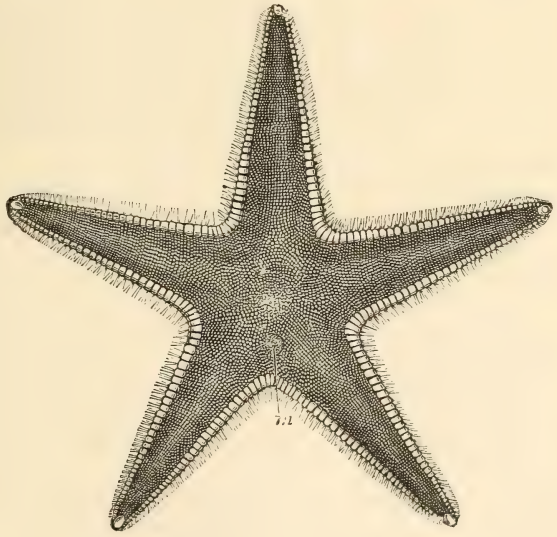

Fig. 269.—*Astropecten irregularis*, viewed from the upper surface; *m* Madreporite. Recent.

rounded by five or more lobes ("arms," or "rays"), which radiate from the body, are hollow, and contain prolongations of the viscera. The body is not enclosed in an immovable box, as in the *Echinoidea*, but *the integument ("perisome") is coriaceous, and is strengthened by*

irregular calcareous plates, or studded by calcareous spines. No dental apparatus is present. The mouth is inferior, and central in position; the anus either absent or dorsal. The ambulacral tube-feet are protruded from grooves on the under surface of the rays.

In their form the Star-fishes differ considerably, though in most the figure is markedly stellate. The animal consists of a central body or "disc," which gives off radiating processes or "arms," but the size of the disc is very different in different species, and the arms vary greatly in length and in number. In many living and extinct forms the "disc" is inconspicuous, and appears to be formed simply by the junction of the bases of the arms, which in this case are normally five in number. The living *Asterias* and *Cribrellæ*, and the extinct *Palæasters* (fig. 270), may be taken as examples of this state of parts. In other forms, as in the Sun-stars (*Solaster*) and the extinct *Lepidasters* and *Plumasters*, the disc is very broad, exceeding or equalling the length of the arms in its diameter; whilst the rays vary in number, from eight or ten up to thirty or more. In the Cushion-stars (*Goniaster* and *Goniodiscus*), again, the body is pentagonal, disc-shaped, and flattened on the two sides, and the arms can only be recognised by the ambulacral grooves on the lower surface (fig. 271).

Fig. 270.—*Palæaster Niagarensis*, Hall. Ordovician.

On the upper surface of the body, placed nearly in the centre of the disc, is the minute aperture of the anus, when this is present; but the genera *Astropecten*, *Ctenodiscus*, and *Luidia* are destitute of a vent. Also on the upper surface is the "madreporite" or "madreporiform tubercle," in the form of a spongy or striated disc placed at the angle of junction of two rays. It has the same function as in the Echinoids, serving to protect the entrance to the water-vascular system. Ordinarily there is a single madreporiform tubercle, but in some genera there are two, three, or more tubercles; and there seems in some cases to be a correspondence between the number of the arms and the number of madreporic plates.

Placed in the centre of the lower surface is the mouth, at the angles of which are five pairs of so-called "oral plates" (fig. 271, *o*), which must not be confounded with plates similarly named in the Crinoids; but there are no teeth. Deep furrows, known as the "ambulacral grooves," radiate from the mouth, one along the under surface of each of the arms, gradually narrowing as the extremity of the latter is approached. The roof of each groove is constituted by a double row of minute calcareous pieces—the "ambulacral ossicles"

—which are movably articulated to one another at their inner ends. Running in the roof of the groove, below the line of union of the two rows of ambulacral ossicles, is one of the radiating ambulacral vessels, from which are given off the rows of suctorial "tube-feet."

The integumentary skeleton of the Asteroids is less developed than in the Echinoids, and has the form of innumerable small calcareous pieces, or "ossicles," united together so as to form a species of chain-armour. The ossicles are generally united with one another in a reticulated manner, and the interspaces between them are filled by the coriaceous integument; but they may be directly united by their edges. In many genera a specially developed series of ossicles forms a row of plates, known as the "adambulacral plates" (fig. 271, *b*), on each side of the ambulacral furrows. In many genera, also, there is a single or double row of large plates, known as the "marginal plates" (fig. 271, *m*), round the margins of the disc and arms, along the line separating the dorsal and ventral surfaces.

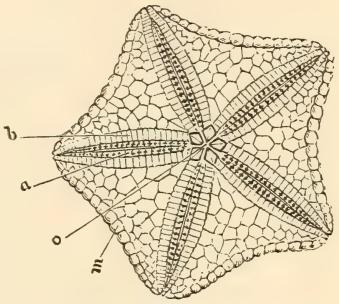

Fig. 271.—Diagram of a Star-fish (*Goniaster*), showing the under surface, with the mouth and ambulacral grooves. *a*, Ambulacral ossicles, with the ambulacral pores between them; *b*, Adambulacral plates, bounding the ambulacral grooves; *m*, Marginal plates (wanting in many species); *o*, Oral plates, placed at the angles of the mouth.

Spines are commonly developed, especially along the margins of the ambulacral grooves, but these structures are in no case movably articulated. The so-called "pedicellariæ" of the Asteroids, as in the Echinoids, may be regarded as peculiarly modified pincer-like spines; but the size of these is too small to render it likely that they can be commonly preserved in the fossil condition. In some genera (as in *Solaster*, *Luidia*, *Ctenodiscus*, &c.), there are large spines the summits of which carry bunches or tufts of minute calcareous processes, and which are known as "paxillæ." In other cases, as in *Pentaceros*, there are very much thickened spines, which may assume considerable dimensions. It is not improbable that the Ordovician fossils upon which the genus *Bolboporites* has been founded, are really of the nature of dermal spines belonging to some Asteroid like *Pentaceros*.

The ambulacral system of the Asteroids is essentially similar in its arrangement to that of the Echinoids. The external opening of the water-vessels is always placed interradially, between the two posterior rays (when five rays are present), and is provided with a porous "madreporite," two, three, or more of these being occasionally present. The madreporite admits the water to the short

"sand-canal," which opens into the circular vessel surrounding the gullet. From the circular canal arise radiating ambulacral vessels, which correspond in number with the number of the arms, and which are lodged, along with the radiating nerves, in deep "ambulacral grooves" on the under surface of the arms. Each radiating vessel gives off two or four rows of cylindrical tube-feet or "pedicels," the ends of which are usually sucker-like, and which are used in locomotion. The tube-feet are protruded by means of vesicles or "ampullæ," which spring from their bases, and are situated superiorly to the radiating vessel. As compared with the Echinoids, the essential peculiarity of the ambulacral system is that the radiating ambulacral vessels are situated externally, and are not covered over by a calcified integument. There are, therefore, no structures in the Asteroids which can be compared with the perforated ambulacral plates of the Sea-urchins, and the tube-feet of the former do not pass through any portion of the integumentary skeleton on the way to the surface. On the other hand, the radiating ambulacral vessels of the Star-fishes are protected by an *internal skeleton*, which is not present in the Echinoids, or which is only imperfectly represented in some types of the latter by the so-called "auriculæ." This internal skeleton has the form of a double

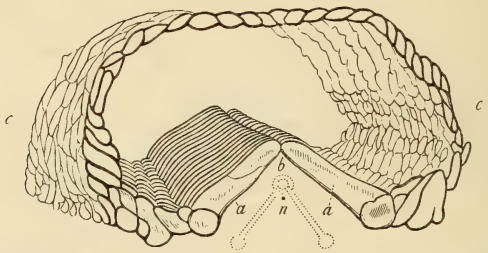

Fig. 272.—Diagrammatic section of the ray of *Asterias rubens*. *a a*, Ambulacral ossicles; *b*, Position of the ambulacral vessel; *c c*, Plates of the external skeleton; *n*, Nerve-cord. The dotted lines show the tube-feet proceeding from the ambulacral vessel, but the ampullæ are not represented.

series of elongated calcareous plates, the so-called "ambulacral ossicles," which form the roof of the ambulacral groove on the under side of each arm, and are so apposed to one another as to form a kind of elongated pent-house, beneath which is placed the radiating ambulacral vessel (fig. 272, *a a*). The ambulacral ossicles on the one side of the ambulacral groove may be directly apposed to the ossicles of the corresponding row on the other side of the groove (as in the typical Star-fishes), or the ossicles of the one row may alternate with those of the opposite row (as in the ancient group of the *Encrinasteriæ*). In either case the ambulacral ossicles are

so excavated on their sides as to give rise by their apposition laterally to a series of pores, by means of which the ampullæ communicate with the bases of the tube-feet. Hence, the ampullæ are situated in the interior of the arms, *superiorly* to the chain of ambulacral ossicles, while the radiating ambulacral vessels and tube-feet are placed *inferiorly* to the same.

In addition to these ambulacral vessels, Star-fishes possess a system of respiratory organs which are known as the dermal branchiæ or "papulæ." These are delicate cæcal processes of the integument, the cavities of which are in direct relationship with the general body-cavity. In one order of recent Star-fishes (*Phanerogonia*) they are restricted to the dorsal surface, while in the *Cryptogonia* they are distributed over the whole body.

The generative organs of the *Asteroidea* are situated within the "arms," above the chain of ambulacral ossicles, and they discharge their products by means of minute sieve-like openings in the angles between the arms, the size of these apertures being too small to admit of their recognition in a fossil condition.

The living Asteroids have a wide range in space, being principally shallow-water forms, but extending from the littoral zone to great depths in the sea. As regards their *distribution in time*, the Star-fishes are a group of great antiquity, the earliest members of the order appearing in the Ordovician (Upper Cambrian?) strata. Most of the Palæozoic types are peculiar, but the recent genus *Astropecten* is stated to occur in rocks as old as the Devonian.

As regards their *classification*, the Asteroids may be divided into two primary groups, or sub-classes, according to the arrangement of the ambulacral ossicles. In one great group (*Euasteroidea*), the two rows of ambulacral ossicles which roof over each ambulacral furrow are placed opposite to each other. The forms of this group are not unrepresented in the Palæozoic rocks, but they are principally characteristic of the Secondary and Tertiary deposits, and are the only types now in existence. On the other hand, most of the Palæozoic Star-fishes belong to the series of the *Encrinasteriæ*, in which the two rows of ambulacral ossicles in each arm are so placed as to alternate with one another. No form belonging to this group of Star-fishes appears to have survived the Palæozoic period. Owing to their rare occurrence as fossils, and their generally imperfect state of preservation, Star-fishes are not of special interest to the palæontological student, and it will be sufficient here to briefly indicate the chief characters of some of the more important of the known fossil forms.

The section of the *Encrinasteriæ*, in which the ambulacral ossicles are alternately placed, is, as above remarked, exclusively Palæozoic, and the widely distributed genus *Palæaster* may be taken as its

central type. In this genus (fig. 273) the body is five-armed, the disc being very small; and the ambulacral grooves on the under side of the arms are furnished with two rows of alternately placed ambulacral ossicles, bounded on each side by a row of "adambulacral plates," which are, in turn, bordered by a series of large "marginal" plates. On the dorsal surface are three or more rows of plates which are united by intermediate ossicles, and do not appear to be separated by intervening pores. The genus *Palæaster* comprises some species of considerable size, and ranges from the Ordovician to the Carboniferous. The Ordovician genus *Urasterella*

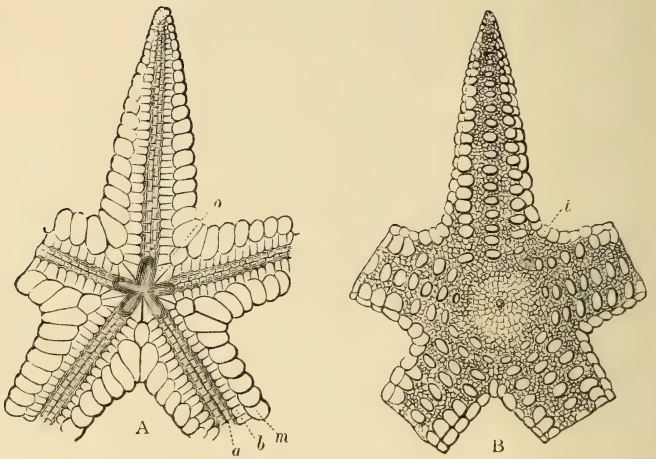

Fig. 273.—*Palæaster eucharis*, Devonian (after Hall). A, Under side of a specimen, four of the arms being cut short; B, Upper side of the same. *a*, Ambulacral ossicles, lying in the ambulacral grooves; *b*, Adambulacral plates; *m*, Marginal plates; *o*, One of the oral plates; *t*, Madreporiform tubercle.

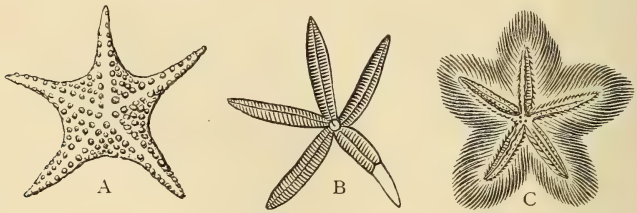

Fig. 274.—A, *Palasterina primæva*, Silurian; B, *Palæaster Ruthveni*, Silurian; C, *Palæocoma Colvini*, Silurian. (After Salter.)

(= *Stenaster*) is in many respects like *Palæaster*, but the ambulacral grooves are bordered by a row of adambulacral plates, without a second row of marginal plates. *Petraster*, also Ordovician, has an incomplete series of disc-plates between the adambulacral and mar-

ginal rows of plates, but is doubtfully separable from *Palæaster*; while the Ordovician and Silurian *Palasterina* (fig. 274, A) has the disc still more extensively developed, and is further distinguished by the fact that the plates of the adambulacral series which are placed at the angles of the oral aperture are large and triangular. The Silurian genus *Palæodiscus*, again, has a discoid form, the body being pentagonal, without distinct arms, and the mouth being furnished with five pairs of triangular oral plates. Lastly, the Silurian genus *Palæocoma* (fig. 274, C) is an aberrant form of this group, with slightly prominent arms, laterally bordered by long spines, the intervals between which are filled up by a netted membrane.

In the Devonian rocks, various forms of the *Encrinasteriæ* have been detected, the chief genus in this formation being *Aspidosoma*, in which the disc is of large size, with five small arms, and the structural characters are in many respects peculiar. Thus, the arms are covered superiorly with two or four rows of closely apposed plates, which are continued over the disc, leaving a central star-shaped space apparently covered only by a leathery skin; while the madreporite is stated to be placed interradially on the under side near the mouth. The known species of this singular genus are found in the Devonian rocks of Germany. *Helianthaster*, of the Devonian rocks of Germany and Britain, is imperfectly known, and may possibly be an Ophiuroid. It has a large disc, and from fourteen to sixteen arms.

The sub-class of the *Euasteroidea* is distinguished from the preceding by the fact that the pairs of ambulacral ossicles are placed opposite to each other, and are directly united by their inner ends. The members of this group appear in rocks as ancient as the Devonian, while all the Mesozoic, Kainozoic, and Recent Star-fishes are referable to this series.

The following classification of the *Euasteroidea* has recently been proposed by Sladen, some of the less important families being omitted :—

ORDER I. PHANEROGONIA.—Marginal plates large and well developed; papulæ restricted to the dorsal surface. Ambulacral plates well spaced; tube-feet in two rows.

Families.—Porcellanasteridæ (*Porcellanaster, Ctenodiscus*), Astropectinidæ (*Astropecten, Luidia*), Pentagonasteridæ (*Astrogonium, Stellaster, Goniodiscus*), Antheneidæ (*Goniaster*), Pentacerotidæ (*Pentaceros*).

ORDER II. CRYPTOGONIA.—Marginal plates inconspicuous; papulæ distributed over the whole body. Ambulacral plates crowded and narrow; tube-feet in two or four rows.

Families.—Solasteridæ (*Solaster, Crossaster*), Pterasteridæ (*Pteraster, Hymenaster*), Echinasteridæ (*Echinaster, Cribrella*), Asteriidæ (*Asterias*), Brisingidæ (*Brisinga*).

The forms of the *Euasteroidea* which have been detected in the Devonian rocks belong mostly to extinct genera (*Xenaster, Eoluidia,*

and *Palastropecten*), but the still existing genus *Astropecten* (*Asterias* of many authors) is represented by a single species (Stürtz), and the same genus is said to occur in the Carboniferous rocks. If some doubt attaches to the Palæozoic forms which have been referred to *Astropecten*, unquestionable remains of species of this genus occur in the Mesozoic and Tertiary rocks, the earliest appearing in the Lias. The genus belongs to the group of Star-fishes (*Phanerogonia*) in which the tube-feet are in two rows and the "papulæ" confined to the dorsal surface, and is recognised by its five-rayed form, and flattened disc and arms, the edges of which carry a double row of large "marginal plates" (figs. 269 and 275). The lower of the two

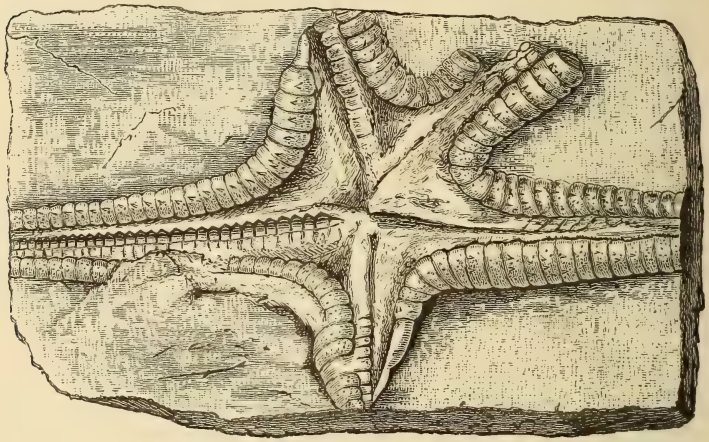

Fig. 275.—Under surface of *Astropecten Phillipsii*, of the natural size. Jurassic. (After Wright.)

rows of marginal plates is furnished with spines, and the whole of the upper surface is covered with tubercles crowned by groups of minute prickles.

Other genera of *Phanerogonia* which are abundantly represented in the Jurassic, Cretaceous, and Tertiary rocks, and which still survive, are *Goniaster*, *Astrogonium*, *Goniodiscus*, and *Stellaster*. The first-named genus comprises the so-called "Cushion-stars," and is characterised by the fact that the body has the form of a pentagonal disc (fig. 271), in which the arms are principally recognisable by the presence of the ambulacral furrows on the inferior surface. The disc is bordered by a double row of large "marginal plates," and the upper and lower surfaces are covered with small, four-sided or polygonal plates. Besides the above, the existing genera *Pentaceros* (*Oreaster*) and *Luidia* appear in the Jurassic, though the occurrence of the latter is not certainly established. Among the *Crypto-*

gonia, the recent genus *Solaster*, comprising the familiar "Sun-stars," is represented by a single known Jurassic species, and is easily recognised by its wide disc and short arms, and by the fact that the dorsal integument is studded at intervals with prominent "paxillæ." Another still living genus, which is known to have existed in rocks as old as the Lias, is *Asterias* (or *Uraster* of many authors). This familiar genus belongs to the group of Star-fishes in which the ambulacral tube-feet are in four rows, and is the only form of this group which has hitherto been found fossil. The disc is small, and the arms are long, and are variable in number, while the dorsal integument is hardened by netted ossicles, many of which are developed into projecting tubercles or blunt spines. The extinct genera of Mesozoic Star-fishes, such as the Jurassic *Plumaster* and *Tropidaster*, do not exhibit any special peculiarities demanding notice here.

Class III. Ophiuroidea.

The class of the *Ophiuroidea* comprises the small but familiar group of the "Brittle-stars" and "Sand-stars," and is characterised by the fact that *the body is stellate, consisting of a central "disc," in which the viscera are contained, and of elongated "arms," which are sharply separated from the disc, do not contain prolongations of the alimentary canal, and are not furnished inferiorly with open ambulacral grooves.*

The body in the Ophiuroids always has the form of a rounded or pentagonal disc (fig. 276), and carries long slender arms, which are typically simple, though they are branched in many of the Euryalids, and which are essentially employed as locomotive and prehensile organs. The arms do not contain diverticula from the alimentary canal, but they lodge the radiating ambulacral vessels and nerve-cords, these structures not being situated in open "ambulacral grooves," as in the Asteroids, but being covered in by the coriaceous or plated integument. On the under side of the body, in the centre of the disc, is seen the stellate opening of the mouth (fig. 276, c); and the reproductive organs open also on the under side by ten fissures or slits, a pair of these being situated at the base of each of the five arms. Owing to the absence of an anus, there is no aperture on the upper surface of the body.

With regard to the integumentary skeleton of the Brittle-stars, it is impossible to enter here into the interesting features shown in the embryonic condition of certain Ophiuroids, at which stage it can be shown that the exoskeleton of the dorsal surface is in many respects homologous with the apical disc of the Echinoids and the calyx of the Crinoids. In the adult condition, the integumentary skeleton of the Ophiuroids is of a very complicated character; but the im-

portance of the group from a palæontological point of view is not sufficient to justify its being treated of here except as regards its general features. The upper surface of the disc of an Ophiuroid is covered throughout with calcareous plates, scales, or granules. A large central plate ("dorsocentral") is sometimes recognisable, and a pair of large plates ("radial shields") is usually developed on the dorsal aspect of the disc at the point of origin of each of the

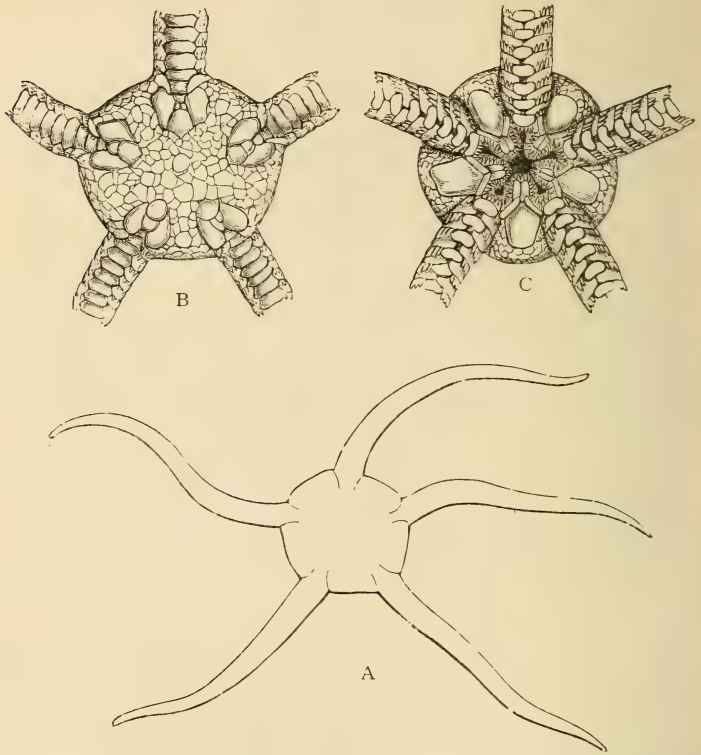

Fig. 276.—Ophiuroidea. *Ophioglypha lacertosa.* A, Outline, of the natural size; B, The disc viewed from above, twice the natural size; C, The disc viewed from below, showing the mouth and genital fissures, twice the natural size. (Original.)

five arms (fig. 276, B). On the under side of the disc the arms, with their ventral rows of plates, are continued to the mouth, but the spaces between the arms ("interbrachial areas") are covered with plates, scales, or minute tubercles of lime (fig. 276, C). The stellate aperture of the mouth is bordered with a system of peristomial ossicles, some of which act as teeth; while at its angles, one in each interbrachial space, are situated five large "mouth-shields"

(fig. 276, c), which are homologous with the "oral plates" of the Crinoids. In the majority of the Brittle-stars one (or more) of the oral plates is enlarged, and represents in function the "madreporite" of the Star-fishes.

The arms are, typically, protected by four rows of calcareous plates, one dorsal, one ventral, and two lateral (fig. 277). The lateral, or "adambulacral," plates carry rows of spines, and not only cover the sides of the arm, but also encroach upon the inferior surface. The ventral shields ("superambulacral plates") are so related to the lateral plates, that a pair of pores is formed on each side of each of the former, by means of which the tube-feet gain the exterior. In the Euryalids, the arms are covered with a leathery skin, containing minute granules and scales.

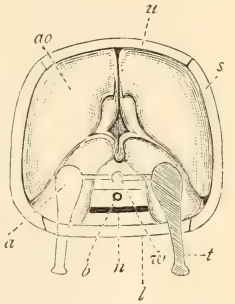

Fig. 277.—Diagram of the cross-section of the arm of an Ophiuroid (slightly altered from Sladen). *ao*, Ambulacral ossicle, immovably united with the corresponding ossicle of the opposite side; *u*, Superior plate of the arm; *s*, Lateral plate; *l*, Inferior plate; *n*, Radial nerve-cord; *b*, Radiating blood-vessel; *w*, Radiating ambulacral vessel; *t*, Tube-foot; *a*, Ampulla.

In addition to the proper integumentary skeleton, the Ophiuroids possess an *internal* or ambulacral skeleton, consisting of a linear series of large calcareous discs or "vertebral ossicles," which occupy the greater part of the interior of each arm, and are grooved inferiorly for the reception of the ambulacral vessel and radial nerve (fig. 277). These discs correspond with the "ambulacral ossicles" of the Star-fishes, but the ossicles of each pair are anchylosed with one another. Successive vertebral discs are movably articulated with one another, and the entire series is largely supplied with muscles. The first two pairs of ambulacral ossicles in each series have their lateral elements disjunct, instead of being fused in the middle line, the pieces of the first pair taking part in the formation of the calcified peristome, and thus becoming connected with the armature of the mouth.

The ambulacral system of the Ophiuroids is constructed upon essentially the same type as in the Asteroids and Echinoids, but its place as a locomotive apparatus is taken by the arms, the tube-feet being tentacle-like, without terminal suckers, and with no specially developed "ampullæ." The special peculiarity of the ambulacral system in the Ophiuroids, as compared with that of the Asteroids, is that the grooves on the under side of the row of ambulacral ossicles, in which lie the radiating ambulacral vessels, are not open, as they are in the latter, but are closed in by the passage over them of the integument. Another peculiar feature, in all except the extinct *Protophiurida*, is the position of the "madreporite" on the inferior

surface of the body and its connection with the oral plates, with one of which it is generally confluent.

As regards the digestive system, the Ophiuroids differ from the majority of the Asteroids in the fact that the alimentary canal terminates blindly, and there is, therefore, no anal aperture upon the dorsal surface of the disc.

Lastly, as regards the reproductive system, the generative glands in the Ophiuroids are placed interradially, and their ducts open into singular folded pouches or "bursæ," which in turn communicate with the exterior by means of slit-like openings (the "genital fissures"), which are placed, singly, or rarely in pairs, on the sides of the arms inferiorly, at their junction with the disc (fig. 276, c). Calcareous plates are sometimes developed in the walls of these bursæ, and currents of sea-water flow in and out of the genital fissures. It is probable, therefore, that these "genital bursæ" are partly respiratory in function, and that they correspond with the so-called "hydrospires" of the Cystoids and Blastoids.

The living Ophiuroids are all inhabitants of the sea, and the marine deposits of almost all the great geological periods have yielded examples of the group, the oldest known forms occurring in Ordovician strata. Most of the remains of Ophiuroids, and particularly those of the more ancient formations, are, however, more or less imperfect, while fossils of this group are, as a rule, exceedingly rare. It will be sufficient here, therefore, to deal with the fossil forms of Ophiuroids very briefly.

The existing Ophiuroids fall naturally into two sections—the *Euryalida* and *Ophiurida*—the characters of which are sufficiently distinct. In the *Euryalida*, the arms may be simple, but are more usually branched, and in either case their integument is leathery, the arms being devoid of the rows of plates so characteristic of the typical Brittle-stars. The type of this group is the genus *Astrophyton* (*Euryale*), comprising the well-known "Medusa-head Stars," characterised by their much-branched arms. The only two extinct genera which appear to be referable to the *Euryalida* are *Eucladia* and *Onychaster*. The former of these is found in the Silurian rocks of Britain, and is characterised by the possession of a granulated disc and of five bifurcating arms. The genus *Onychaster* (fig. 278) is based upon forms found in the Carboniferous Limestone of North America, and is characterised by the possession

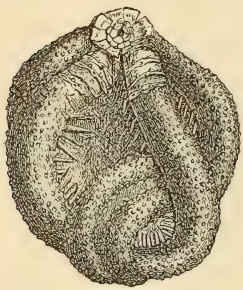

Fig. 278.—*Onychaster flexilis*, viewed sideways, of the natural size, with the arms rolled up. From the Carboniferous Limestone of Indiana. (After Meek and Worthen—copied from Zittel.)

of a small disc, and of five simple round arms, which are covered with a granulated integument, and carry spines on their ventral aspect. As in the living Euryalids, the arms could be rolled up towards their ventral side at their tips.

The second section of the living Ophiuroids—that of the *Ophiurida*—comprises the typical forms of the order, and is characterised by the fact that the arms are always simple and are protected by four rows of integumentary plates (fig. 279). The integument of the disc

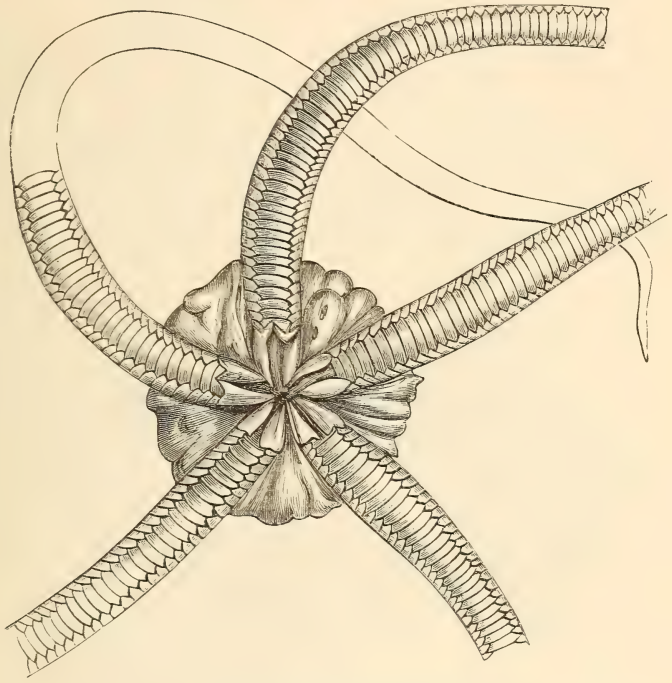

Fig. 279.—Under surface of *Ophioderma* (*Ophioglypha ?*) *Gaveyi*, of the natural size. Jurassic (Lias). (After Wright.)

is soft, or is covered with granules or plates of carbonate of lime. The earliest types of this group appear in the Lower Devonian (*Ophiurella primigenia*, Stürtz); and numerous forms are found in the Secondary and Tertiary rocks. A well-known Triassic genus is *Aspidura* (=*Acroura*), the remains of which are widely distributed in the Muschelkalk (fig. 280). The Jurassic Ophiuroids belong principally to the genera *Ophioderma* (fig. 279), *Ophioglypha*, and *Geocoma*, of which the last is peculiar to the Jurassic rocks, while the two former are represented in the Cretaceous and Tertiary rocks,

and survive at the present day. The recent genus *Ophiolepis* is found in the Pleistocene, and possibly occurs in Tertiary deposits also.

Finally, there are various Palæozoic Ophiuroids which cannot be included in either of the preceding sections, and which may be

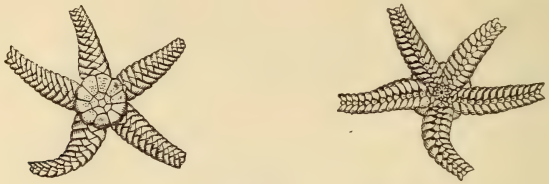

Fig. 280.—*Aspidura loricata.* Muschelkalk.

provisionally placed in a special division (*Protophiurida*), though their characters are not completely understood. All the forms here in question agree with the typical Ophiurids in having five simple plated arms, but the "madreporite" is placed on the dorsal aspect of the body, and the under surface of the arms exhibits a double,

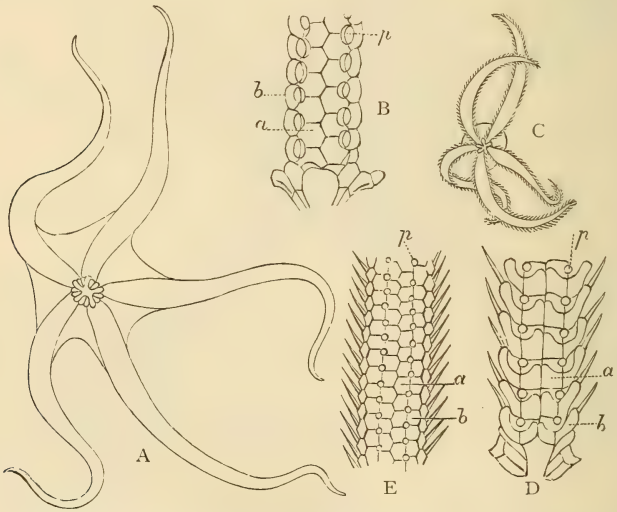

Fig. 281.—A, Outline of *Eugaster Logani*, of the natural size—Devonian. B, Base of an arm of the same viewed from below, enlarged. C, Outline of *Protaster Forbesi*, of the natural size—Silurian. D, Base of an arm of same, viewed from below, enlarged. E, Portion of the arm of *Ptilonaster princeps*, viewed from below, enlarged—Devonian. *a*, Ventral (superambulacral?) plates; *b*, Adambulacral plates; *p*, Pore. (After Hall.)

in place of a single, row of plates (fig. 281, B). Two views may be held as to the nature of the double (or sometimes quadruple) row of plates exhibited on the under side of the arms of the Protophiurids. On one view, these plates are considered as being integument-

ary, and as corresponding with the ventral shields ("superambulacral plates") of the normal Ophiuroids, their special peculiarity on this theory of their nature being their duplication. On the other hand, it may be held that the ventral or superambulacral plates of the ordinary Brittle-Stars are not developed at all in the ancient types in question, and that the double row of plates above alluded to are really the "ambulacral ossicles" or "vertebral discs," which would, on this view, differ from the corresponding structures in the normal Ophiuroids by being separate, instead of being anchylosed in pairs. If this latter view be correct, the Protophiurids may have either had open ambulacral grooves, as in the Asteroids, or the under side of the arms may have been closed by soft skin, as in the Euryalids. Whichever of these two views is the correct one, the plates of the double ventral row of the Protophiurids may either be placed opposite one another, or they may alternate, and they are also so disposed as to give origin to a double series of pores.

Of the genera of Protophiurids, *Protaster* (fig. 282) is found in the Ordovician and Silurian rocks, and is characterised by its round scaly disc, and by the fact that the arms are provided inferiorly with a double row of plates, and carry bunches of lateral spines (fig. 282, B). In the Devonian genus *Eugaster* (fig. 281, A) the general structure is very similar to that of *Protaster*, but the disc is prolonged along the bases of the arms, and the plates of the disc are articulated by their edges, and do not overlap. The under side of the arms (fig. 281, B) exhibits a double row of alternating plates, and lateral spines appear to have been wanting. In the genus *Ptilonaster*, again, the arms exhibit on their under surface *four* rows of plates and a double row of pores. This genus is also Devonian. Lastly, the genus *Tæniaster*, from the Ordovician rocks of Canada, is in many respects like *Protaster*, but the two rows of plates which occupy the under sur-

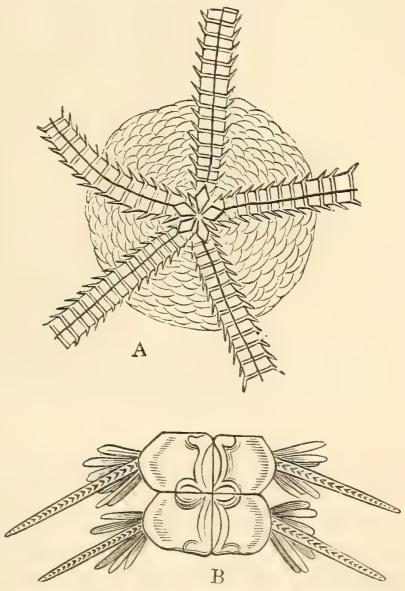

Fig. 282.—*Protaster Sedgwickii*. Silurian. A, Disc and bases of the arms, magnified; B, Portion of an arm, greatly enlarged. (After Salter.)

face of the arms have the peculiarity that each is constricted in the middle, a feature which would rather lead to the belief that these plates are truly of the nature of "ambulacral ossicles."

Class IV. Holothuroidea.

The class of the *Holothuroidea* includes the animals usually known as "Sea-cucumbers," distinguished from the other Echinoderms by their elongated, vermiform, or slug-like form, and their leathery muscular integuments. The mouth and anus are usually terminal in position, and the radial symmetry of the body is not conspicuously shown externally except by the crown of oral tentacles, and, often, by the bands of tube-feet. Palæontologically speaking, the Holothurians are of little importance, since they possess few structures which are capable of preservation in a fossil condition. Unlike the other Echinoderms, the Holothurians exhibit a very limited tendency to a calcification of their tissues. No proper "test," in fact, exists in any Holothurian, but the skin contains numerous isolated, mostly microscopic bodies, of special forms in different types. These calcareous structures (fig. 283) may be globular, wheel-shaped, spicular, anchor-shaped, &c., and

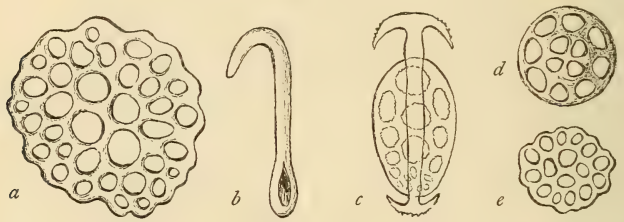

Fig. 283.—Integumentary ossicles of recent and fossil Holothurians. *a*, A plate of *Achistrum Nicholsoni*, enlarged forty-five times, from the Carboniferous rocks of Scotland; *b*, Hooklet of the same, similarly enlarged; *c*, Anchor and anchor-plate of a recent species of *Synapta*, enlarged; *d*, Plate of *Chirodota? Traquairii*, enlarged forty-five times, from the Carboniferous rocks of Scotland; *e*, Plate of the recent *Thyonidium pellucidum*, enlarged. (After R. Etheridge, jun.)

in rare cases (as in *Psolus*) have the form of comparatively large imbricated scales, which constitute a kind of external shell. Whenever the integumentary calcifications are plate-like, they exhibit under the microscope the peculiar netted structure which is characteristic of the Echinodermal test. In addition to the integumentary hard structures, there exists a ring of calcareous pieces surrounding the mouth, and serving for the attachment of five great longitudinal muscles.

Owing to their want of hard structures of any size, the geological history of the Holothurians is necessarily a very imperfect one, being

based only on the occasional recognition of the microscopic plates or spicules of the integumentary skeleton. The oldest remains which can be certainly affirmed to be those of Holothurians are the microscopic plates and spicules described by Mr R. Etheridge, jun., as occurring in the Carboniferous rocks of Scotland. Some of these have the form of rounded, perforated calcareous plates, about $\frac{1}{45}$ inch in diameter, associated with simple calcareous hooks or one-fluked anchors, the shaft of the anchor having a perforation or "eye" at its base (fig. 283, *a* and *b*). These plates and hooklets have been referred to a special genus under the name of *Achistrum;* and they may be compared with the anchors and anchor-plates of the living genus *Synapta* (fig. 283, *c*). Others have the form of circular, generally concavo-convex, wheel-like plates, about $\frac{1}{100}$ inch in diameter, with a group of central pores and a series of marginal perforations (fig. 283, *d*). These resemble the wheel-shaped integumentary plates of such living types as *Thyonidium* (fig. 283, *e*) or *Chirodota*, and they may be provisionally placed in the latter genus.

It is probable that investigations conducted with sufficient care will ultimately show that the minute plates and spicules of Holothurians have been more generally preserved in the fossil condition than has been usually assumed to be the case. In the meanwhile, with the exception of the remains above noted, no undoubted traces of the former existence of Holothurians have been found until the Jurassic rocks are reached. Here, the occurrence of minute wheel-like plates, resembling the "wheels" of the recent *Chirodota* has been recorded. Pocta has described plates of *Psolus* from the Chalk of Bohemia, and Schlumberger has recently found the characteristic armature of *Synapta*, *Chirodota*, and *Thyonidium* in the Middle Eocene of the Paris basin; while *Chirodota* occurs in the Pliocene of Northern Italy, and plates belonging to *Psolus* have been found in Post-tertiary deposits in Bute.

CHAPTER XXV.

DIVISION B. PELMATOZOA.

The three groups of Echinoderms known as the Crinoids, Cystoids, and Blastoids agree with one another in certain common characters, and may be included in a single primary section termed *Pelmatozoa*. In all these forms the body is fixed, either temporarily or permanently, by the dorsal surface, often having a jointed stem or peduncle; and the mouth is placed on the opposite side of the body. In its fully developed condition, the peduncle has the form of a jointed stem, containing a neuro-vascular axis in its interior. The body itself is enclosed in a variously modified series of calcareous plates, which represent the apical disc of the Echinoids, and the upper surface may be provided with jointed appendages (the "arms"). The circular ambulacral vessel has no direct communication with the exterior, or only a limited one, and the radiating ambulacral vessels (when present) are respiratory in function, and are not subservient to locomotion.

Class I. Crinoidea.

The Crinoids or "Sea-lilies" may be defined as Echinoderms in which *the body is fixed, during the whole or a portion of the existence of the animal, to the sea-bottom by means of a jointed, flexible stalk or peduncle, which springs from the centre of the dorsal or aboral surface. The body is cup-shaped or discoidal, and its dorsal surface is protected by a system of calcareous plates. The mouth is situated on the upper surface, generally in the centre. From the margin of the cup-shaped body spring jointed flexible appendages or "arms," which are primitively five in number, and which carry lateral jointed processes or "pinnules." The upper or ventral surfaces of the arms are furnished with grooves corresponding with the "ambulacral grooves" of the Asteroids. The water-vascular system has only a limited communication with the exterior, and is not connected with locomotion. The*

reproductive organs are situated beneath the skin in the grooves on the ventral surface of the arms or pinnules.

As the study of the fossil Crinoids is attended with considerable difficulties, it may be well to give here a brief account of the general anatomy and development of one of the "Feather-stars" (*Comatula*), no other recent type of the group being readily obtainable for purposes of investigation. All the known Crinoids are attached to foreign bodies by a jointed stem or "column" in their young condition; but in the adult state they may either retain this stem of attachment, and thus remain permanently fixed, or they may become

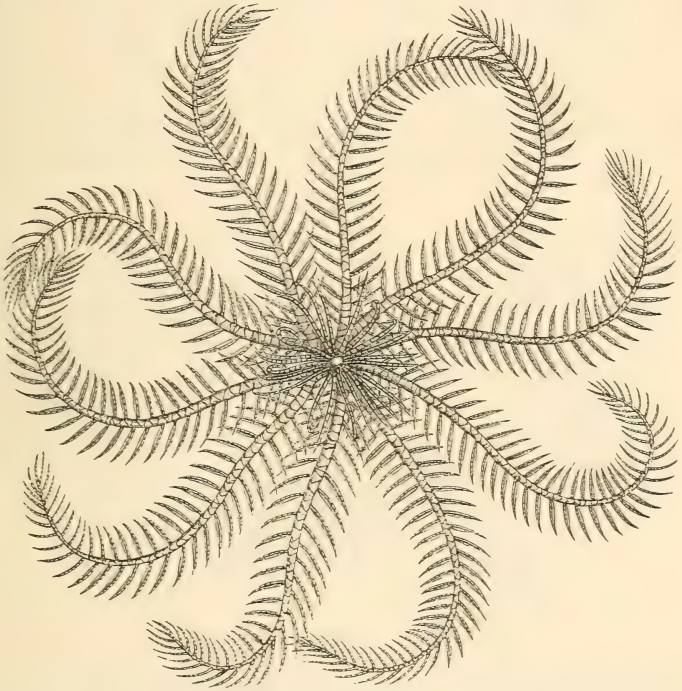

Fig. 284.—Crinoidea. *Antedon* (*Comatula*) *rosacea*, a free Crinoid, viewed from its dorsal or aboral aspect.

detached from the stem and may lead a free existence. In accordance with this, the Crinoids may be divided into the two groups of the "Pedunculate Crinoids" and the "Free Crinoids." In the Pedunculate Crinoids, where the stalk of attachment is permanently retained (fig. 289), the animal may be compared with a Star-fish turned upside down, the column springing from the centre of the "dorsal" (or "abactinal") surface, while the "ventral" (or "ac-

tinal") surface, with the mouth-opening, is turned upwards. In the Free Crinoids, in which the adult is devoid of a peduncle of attachment, the animal has it in its power to move about freely by swimming; while it can at the same time assume the position characteristic of the Stalked Crinoids, since it can fix itself to foreign objects with the mouth turned upwards and the dorsal surface directed downwards.

The "Feather-stars," as exemplified by the common *Antedon* (*Comatula*) *rosacea* of British seas (fig. 284), belong to the group of the "Free Crinoids," being attached by a stalk in their young state only. The adult animal is free, and consists of a pentagonal or cup-shaped body or "calyx," which gives origin on its sides to five jointed processes or "arms." The calyx encloses the visceral mass or disc, the upper or "actinal" surface of which exhibits the apertures of the mouth and anus. The five "arms" bifurcate almost immediately after their origin from the calyx, so as to give rise to ten long slender processes, which are transversely jointed, and

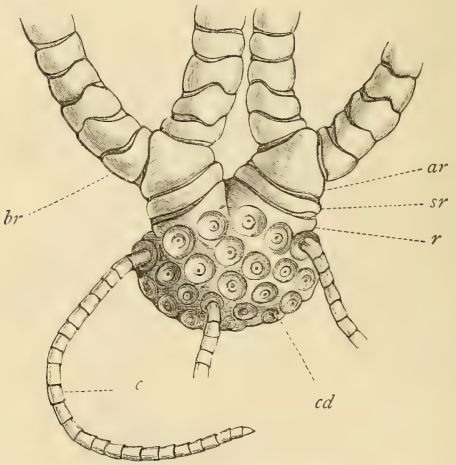

Fig. 285.—Side-view of the calyx of *Antedon* sp., enlarged, the cirri being mostly removed, and the bases of only two rays being shown. *cd*, Centrodorsal plate, with the origins of the dorsal cirri (*c*); *r*, One of the "primary radials"; *sr*, One of the "secondary radials"; *ar*, One of the "axillary radials," carrying the bifurcations of the arm; *br*, First "brachial" plate. (Original.)

are fringed on both sides by delicate filaments or "pinnulæ." The dorsal surface of the body carries a number of delicate jointed flexible processes (figs. 284 and 285, *c*), which are attached to the so-called "centrodorsal" plate, and are known as the "cirri." By means of these the animal can moor itself temporarily to foreign objects, with the mouth turned upwards.

The dorsal or aboral integument is hardened in *Antedon* by the formation within it of a system of calcareous plates, which collectively constitute the "cup" or "calyx," and which in large part correspond with the "apical disc" of the Echinoids. The central piece of the calyx is known as the "centrodorsal" plate (fig. 285, *cd*), and is developed from the topmost joint of the stem in the young Feather-star. It carries the cirri, and has soldered on to it five "radial" plates (fig. 285, *r*), which represent the "ocular plates" of the Echinoids. There are thus *apparently* no representatives of the "genital plates" of the Echinoids. In the great majority of the recent Feather-stars, however, these plates are really present, though they exist only in a metamorphosed condition. They are, in fact, fused together to form a so-called "rosette-plate," which is concealed from view externally, and lies hidden between the centrodorsal and radial plates. This "rosette-plate" consists, therefore, of the amalgamated interradial plates which are known as the "basals" in the stalked Crinoids. Following the first cycle of

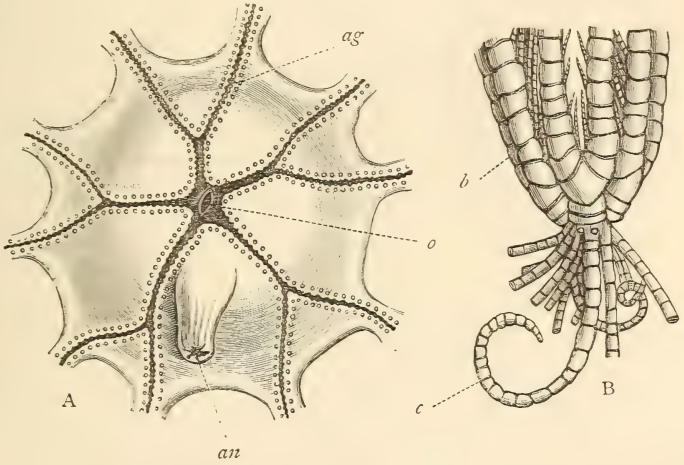

Fig. 286.—A, Ventral or actinal surface of the body of *Comatula* (*Antedon*) *rosacea*, enlarged, showing the central mouth (*o*), the excentric, proboscidiform anus (*an*), and the brachial grooves (*ag*), continued from the bases of the arms across the disc to the mouth. B, Side-view of the lower part of *Antedon lævis*, showing the calyx, the bases of the arms (*b*), and the roots of the dorsal cirri, a single cirrus (*c*) being left complete, enlarged. (After P. Herbert Carpenter.)

"radials" in *Antedon* are two other circles of radial plates (the "second radials" and "axillary radials"), the outermost circle carrying the bases of the jointed arms (fig. 285, *sr* and *ar*).

The upper or ventral surface of the body is covered with an imperfectly calcified, coriaceous skin, and carries the aperture of the mouth. In *Comatula rosacea* the mouth is central (fig. 286, A, *o*),

as it is in all the ordinary Crinoids; but in some Feather-stars (species of *Actinometra*) it may be quite excentric. The anus (*an*) is usually supported on a tubular projection, and is excentric in position. The arms of *Comatula rosacea* exhibit on their ventral surface a deep furrow or groove, the elevated margins of which are cut out into minute crescentic respiratory leaves, at the base of each of which is a group of three tentacles, connected with a cavity in the interior of the respiratory leaf, and communicating by a common trunk with the radiating water-vessel. The floor of the ambulacral furrows is ciliated, and underneath each runs a radiating water-vessel, together with a blood-vascular trunk, and a nerve-band which is in intimate relation with the ambulacral epithelium. In the centre of the arm, between the calcareous skeleton and the water-vessel, are three tubular prolongations of the body-cavity. The middle and largest one of these (fig. 287, *ov*) contains one of the generative glands; while the upper and lower (the "subtentacular" and "cœliac" canals) are much smaller, and permit of a circulation of water derived from the body-cavity. The slender lateral "pinnules" carried by the arms, as regards their internal anatomy, have precisely the structure of the arms themselves.

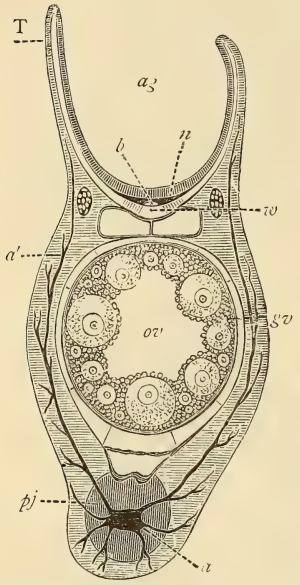

Fig. 287.—Cross-section of a pinnule of the Arctic Feather-star, magnified seventy-five times. (From Ludwig, after P. H. Carpenter.) *pj*, Calcareous skeleton, containing the axial nerve-cord (*a*); *ag*, Ambulacral groove; *n*, Radial nerve; *b*, Radial blood-vessel; *w*, Ambulacral vessel; T, Tentacle; *ov*, Ovary, with the subtentacular canal above, and the cœliac canal below; *gv*, Genital blood-vessel.

The ciliated grooves on the ventral aspect of the arms are continued over the upper surface of the disc to reach the subcentrally or excentrically placed mouth; and the animal feeds upon the minute organisms conveyed to the mouth by the water-currents set up along these grooves. The mouth opens into a spirally coiled alimentary tube, which forms most of the so-called "visceral mass," and is wholly contained within the calyx, no diverticula from it extending into the arms.

The water-vascular system consists of a circumoral ring, and of the radiating water-vessels, which run along the brachial furrows. These give off the tentacles, which are destitute of suckers, and are essentially respiratory in function. The circular ring communi-

cates by numerous water-tubes with the body-cavity, to which the sea-water is freely admitted by minute pores in the body-wall; while some of these pores are said by Perrier to lead directly into the oral water-vascular ring, though this is denied by Hamann.

The vascular system is extraordinarily developed, and its upper portion consists of an oral ring, which gives rise to the radial vessels, and is also connected with a peculiar organ apparently serving as a kidney, as well as with numerous "intervisceral" vessels. There is no aboral vascular ring, but the vessels become connected inferiorly with a singular quinquelocular structure known as the "chambered organ," which is contained within the centro-dorsal plate of the calyx. The chambered organ is enclosed in a peculiar fibrillar sheath, the nature of which will be spoken of immediately, and it sends prolongations into all the arms, along canals contained within the skeleton of the latter, and also into the dorsal cirri.

In the Crinoids generally, the structure of the vascular system is, up to a certain point, much the same as it is in *Comatula*. Occupying the dorsoventral axis of the body is the lobated kidney, enclosed in a sheath of vessels. Dorsally, these resolve themselves into a central group (of one or more), and five peripheral vessels, the latter expanding in the lower part of the calyx into the five chambers of the "chambered organ." In the Pedunculate Crinoids the chambers narrow again, and the group of vessels is continued down the central canal of the column. In *Pentacrinus*, which has cirri at regular intervals, the five peripheral vessels expand in each cirrus-bearing joint into five dilatations, which thus give rise to a miniature "chambered organ," each chamber of which gives off a single vessel to a cirrus.

The nervous system of the Feather-stars is also extraordinarily developed as compared with that of the other Echinoderms. As has been previously seen, there is found under the floor of each of the brachial grooves a fibrous nerve-band (fig. 287, *n*), which corresponds morphologically with one of the radiating nerve-fibres of a Star-fish. In addition to these ambulacral nerves, the "chambered organ," above spoken of in connection with the vascular system, is enclosed in a peculiar fibrillated sheath, which has been shown by Dr W. B. Carpenter to be of a nervous nature. It gives off a series of radial prolongations or "axial cords" (fig. 287, *a*), which occupy median canals within the skeleton of the arms and pinnules, and send numerous branches to the muscles and the integument (fig. 287, *a'*). In the stalked Crinoids the fibrillar nerve-sheath is likewise prolonged, along with the blood-vessels, into the central canal of the column or peduncle. No representative of this peculiar system of nerves is known in the unstalked Echinoderms (*Echinozoa*).

Though free in its adult condition, the Rosy Feather-star passes through a stage of its development in which it is attached by a delicate jointed stalk to some foreign object (fig. 288). When first discovered in this condition, it was supposed to be a distinct type of the Crinoids, and was described under the name of *Pentacrinus Europæus*. The *Comatula*, therefore, represents temporarily, in this stage of its development, the permanent condition of the Pedunculate Crinoids.

As regards the development of *Comatula*, the larva is at first cylindrical, with four transverse bands of cilia, a hinder tuft of cilia, and an alimentary canal furnished with a lateral aperture, its general aspect closely resembling that of the embryos of certain Annelides. The skeleton of the calyx is developed anteriorly, that of the column posteriorly, the former being the first to appear. In its early condition (fig. 288) the calycine skeleton consists of a row of five "basal" plates (*b*), together with three or five small "underbasals," which rest below upon the so-called "centrodorsal plate" (*cd*), and fuse with it at an early period. The basals are succeeded above by a cycle of five "oral" plates (*o*), in the centre of which the permanent mouth is finally developed. Five "radial" plates (*r*) are next developed as a cycle between the oral and basal plates: and to the radials are rapidly added the plates of the arms proper (the "brachials). Inferiorly, the centrodorsal plate rests upon a short jointed column (fig. 288, *c*), at the bottom of which is an expanded "dorsocentral" plate (*d*), forming a disc of attachment; and the larva now passes into what is known as its "Pentacrinus stage." In the further progress of growth the arms increase in length, and the oral plates diminish in size and ultimately disappear. At the same time the centrodorsal plate increases in size, so as to enclose the basal plates, which in turn become fused with one another, and remain only as the so-called "rosette" on the upper surface of the centrodorsal. The latter also develops jointed cirri from its outer suface, and finally becomes detached from the next joint of the column below, when the animal enters upon its free stage of life.

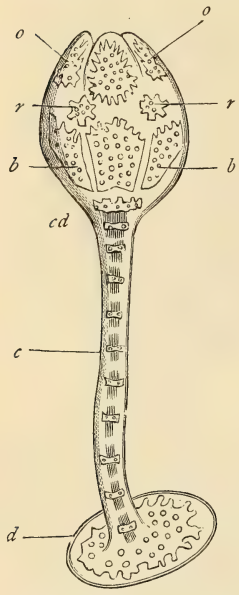

Fig. 288.—Larva of *Comatula* (*Antedon*) *rosacea*, enlarged (after Sir Wyville Thomson). *o o*, Oral plates; *r r*, Radial plates; *b b*, Basal plates; *cd*, Centrodorsal plate; *c*, Column; *d*, Disc of attachment (dorsocentral plate).

As regards the essential features in their anatomy, the "Stalked" Crinoids do not differ materially from the "Free" forms of the group. More particularly, there is a substantial identity in structure in the two sections of the order as regards the form and arrangement of the alimentary canal, the ambulacral and vascular systems, and the nervous and reproductive organs. As the majority of the fossil Crin-

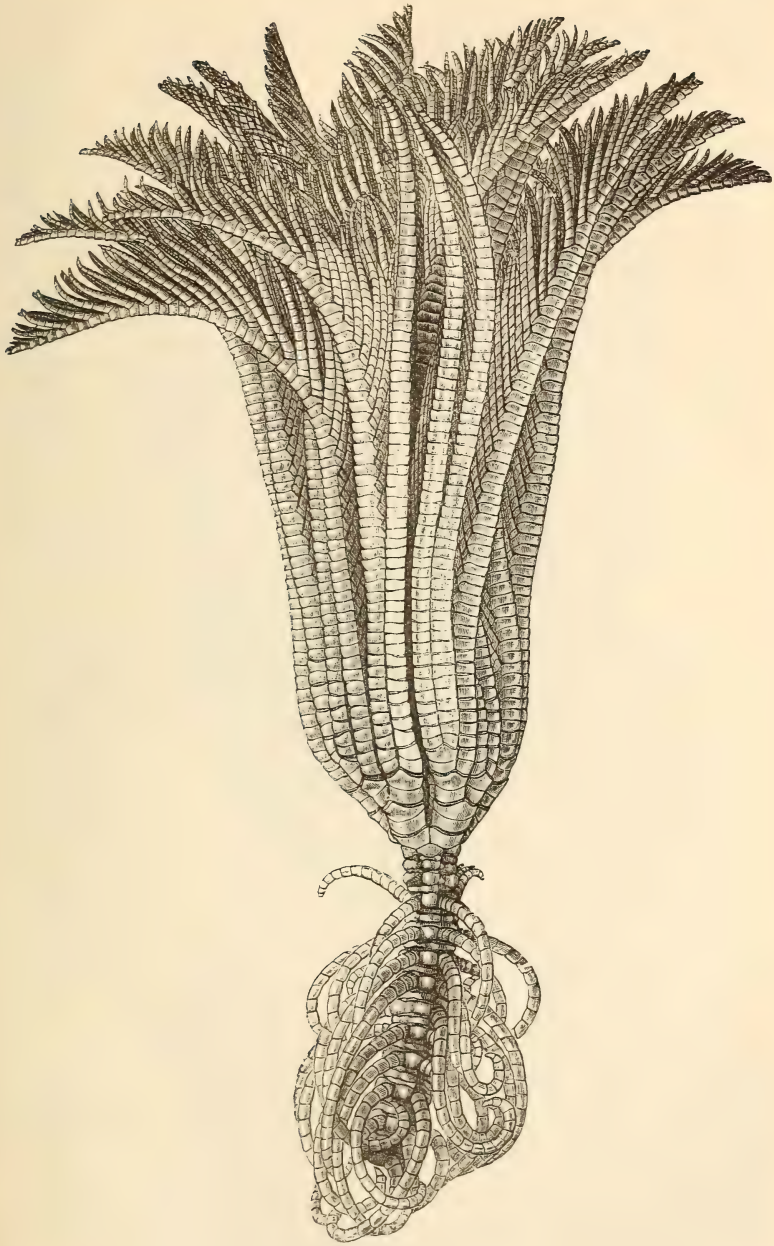

Fig. 289.—*Pentacrinus Macleayanus*, a living stalked Crinoid, slightly enlarged.

oids, however, belong to the Pedunculate division of the group, it is necessary to study the skeleton of these in greater detail.

A pedunculate Crinoid, such as *Pentacrinus* (fig. 289), consists of a cup-shaped body or "calyx," which encloses the principal viscera, and is furnished with a crown of pinnate "arms," and which is attached to some foreign object by means of a stalk or "column," composed of a number of calcareous pieces or "articulations." In some cases (as in *Apiocrinus*) the base of the "column" is considerably expanded. In other cases the column is simply "rooted by a whorl of terminal cirri in soft mud" (Wyville Thomson). The column may be extremely short, or even wanting in the adult, or may reach the extraordinary length of sixty or seventy feet. The whole column is composed of a series of ring-like or pentagonal joints, which are generally movably articulated with one another, and are furnished with special muscles, the joint-surfaces often having a very elaborate structure, and the entire stem possessing in the living state a larger or smaller amount of flexibility. Very often more or fewer of the column-joints carry lateral jointed processes or "cirri" (fig. 289). Each joint of the stem, further, is perforated centrally by a canal, which lodges an extension from the "chambered organ" and its fibrillar nerve-sheath.

As regards its shape, the "column" of the Stalked Crinoids is very commonly round, but it is sometimes oval or elliptical (as in *Platycrinus*, fig. 300), and it is not infrequently pentagonal (as in *Extracrinus*, fig. 290). The separate joints or "articulations" of the column are usually so connected with one another that whilst the amount of movement between any two pieces must be very limited, the entire stem is more or less flexible. The articular surfaces or facets by which contiguous joints are connected, are differently marked in different cases. In many forms, the articulating facets are marked by more or less numerous radiating striæ, which run from the central canal of the joint to its margin. In other cases, as in *Pentacrinus* and *Extracrinus* (fig. 290), the articular faces are united by crenated ridges arranged in a pentapetalous figure. Though usually articulated movably, the stem-joints are occasionally united here and there by the peculiar mode of union known as "syzygy." By this is understood the immovable union of two originally separate joints by close ligamentous connection and subsequent more or less complete fusion, the primitive line of division usually remaining visible as a line of suture.

The uppermost joint of the column is often larger than, and differently shaped from, the inferior joints, and may, as in *Apiocrinus*, enter largely into the formation of the calyx. In many cases, as in *Pentacrinus* and *Extracrinus* (figs. 289 and 290), the column is furnished with more or less numerous auxiliary arms or "side-arms," which represent the "cirri" of the Comatulids. The column generally increases in height by the addition of new joints at its summit, and also by the intercalation of others between those previously formed in the upper, and therefore the youngest, part of the stem; and the whole series is traversed centrally by a variously shaped tube—the misnamed "alimentary canal" of old writers

—which, as previously noted, lodges the neuro-vascular axis of the stem. The neuro-vascular tube of the stem sends off diverticula into the cirri and root-like processes of attachment, when these structures are present. It is very commonly round, but it may be pentapetalous. In some cases, there are four or five canals running parallel with and around a central tube, but in this case the function of the outer circle of tubes is uncertain.

Fig. 290.—*Extracrinus briaroides*, from the Lias, showing the crown of arms, and the column with its side-arms. The small figures show the stem-joints of *Extracrinus subangularis*.

The column carries at its summit the cup-shaped, pyriform, or bursiform body of the animal, or "calyx" (fig. 291). As the column is produced from the aboral pole of the animal, it is the

dorsal side of the calyx which is turned downwards, while the ventral or oral side is turned upwards. The dorsal or inferior side of the calyx is entirely enclosed in a series of polygonal calcareous plates, which are more or less closely joined together. In some cases the plates are united by firm sutures; while in others the plates are more or less movably articulated; and in still other cases certain of the plates may be connected by the peculiar mode of immovable union, which has been already described under the name of "syzygy." In rare cases, as in the Devonian genus *Hystricrinus*, the calycine plates are furnished externally with movably articulated spines, resembling the prickles of the Echinoids.

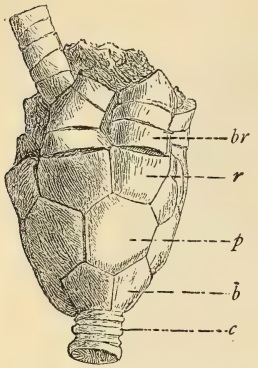

Fig. 291. — Side-view of the calyx of *Poteriocrinus multiplex*, from the Carboniferous Limestone of Russia, of the natural size, showing the top-joints of the column (*c*) and the bases of the arms. *b*, The cycle of "underbasals"; *p*, The "basals"; *r*, The "primary radials"; *br*, The "second radials" (or first "brachials" of some authors). (After Zittel.)

The following is the general arrangement of the calycine plates in the Stalked Crinoids (figs. 291 and 292). Resting directly upon the summit of the highest joint of the column is the cup-shaped basal portion of the calyx, which is known as the "basis," and which may consist of a single or double row of plates. In those Crinoids in which the basis is composed of a single row of plates only — hence termed "monocyclic" Crinoids—its component plates rest directly upon the top-joint of the column, and are known as the "basals." The "basals" are interradial in position, and are homologous with the "genital plates" in the apical disc of the Echinoids. The basals are usually five in number, but may be reduced to four, three, or two; and they may be invisible externally owing to their concealment by the radials (as in most *Comatulæ*). In the so-called "dicyclic" Crinoids, on the other hand, the true "basals" retain their constant interradial position, but are separated from the top-joint of the column by an intercalated row of plates termed the "underbasals" (figs. 291 and 292, *b*), the basis thus consisting of two successive cycles of plates.[1] The underbasals are radial in position, and have no representative in the calyx of the "monocyclic" Crinoids. It is not clear that they possess any homologues in the apical disc of the Sea-urchins, as do the basals and radials of the Crinoidal calyx. They were formerly compared

[1] In the nomenclature of some writers, the plates of the dicyclic calyx are known respectively as the "basals" and "parabasals"; but the nomenclature of Dr P. Herbert Carpenter, employed above, undoubtedly expresses the true homologies of the monocyclic and dicyclic forms.

collectively to the "suranal" or dorsocentral plate of the *Saleniadæ*, which is represented in the larvæ of other Urchins; but it is now generally admitted that the homologue of this plate in the Crinoids is the plate supporting the discoidal base of the larval stem (fig. 288, *d*). Succeeding the basals, and alternating with them, are one or more cycles of plates, which are directly superimposed upon one another in longitudinal rows, and which form the foundations of the arms. The lowest of these, up to the first bifurcation, are known as the "radials" (figs. 291, 292, *r*), and are termed "primary," "secondary," or "tertiary" radials, according to their distance from the basals. The last

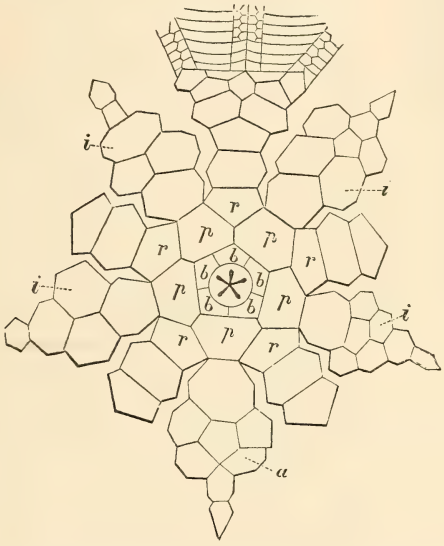

Fig. 292.—Diagram of the dissected calyx of *Rhodocrinus*, a "dicyclic" Crinoid, viewed from below (after Schultæ). *b*, Underbasals; *p*, Basals; *r*, First radials; *i*, Interradials; *a*, Anal plates.

radial plates, or those furthest from the column, are the "axillary" radials, and give origin to the lowest plates of the arms ("brachial" plates); or, if the cycle of the primary radials alone is developed, the first brachials rest upon these. The "radial" plates are arranged in a series of five vertical columns, which are, as the name implies, radial in position; and the primary radials are homologous with the "ocular plates" in the apical disc of the Echinoids.[1]

[1] From the strict morphological point of view, these primary radials are the only plates to which the name "radials" is applicable, all those which follow them being really arm-joints ("brachials"). It is, however, convenient for descriptive purposes to give the name of "radials" to all those plates which are

Between the five columns of radial plates, corresponding with the five arms, there may be intercalated certain other smaller plates, which, from their position, are spoken of as "interradials" (fig. 292, *i*). When "interradials" are developed, one of the interradial spaces, corresponding with the anus, is usually wider than the others, and is furnished with an additional series of calcareous pieces, which are termed "anal plates" (fig. 292, *a*).

As above mentioned, the first brachial plates rest directly upon the highest row of radials; and the "arms," therefore, spring from the margins of the calyx, where the dorsal and ventral surfaces join. The arms are formed of a single or double longitudinal row of "brachial ossicles," the plates in the latter case alternating with one another. The brachial plates are in many cases traversed by a single or double canal, which transmits the axial nerve-cord (fig. 287). In most cases, the brachial ossicles are movably articulated with one another, having their opposed surfaces separated by interarticular substance, and being provided with muscular fasciculi. In other cases, however, the arm-plates are fixed in immovable junction by "syzygy," and may coalesce with one another. The arms are primarily five in number, and they may remain simple. Most commonly, however, the arms are more or less branched, and they generally carry on their sides short, jointed filaments or "pinnules," the structure of which repeats that of the arms on a smaller scale (fig. 293). Pinnulæ may be wanting (as in *Cyathocrinus*), and it is not always easy to distinguish between "pinnules," properly so called, and "armlets" (*i.e.*, short divisions of the arms themselves); since the real distinction between these structures depends upon their contained soft parts, and is therefore unavailable as regards fossil forms. The proper "arms," namely, lodge the sterile genital cord, while it is within the pinnules that the fertile portions of the genital glands are contained. Owing to the position of the reproductive glands beneath the soft skin of the pinnules, it follows that there exists no generative opening, or "ovarian aperture," in the walls of the calyx, such as is present in the Cystideans.

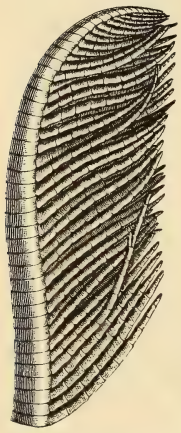

Fig. 293.—Portion of an arm of *Platycrinus*, showing the lateral pinnulæ.

The ventral surfaces of the arms and pinnules, as in *Comatula*, are furnished with furrows—the "ambulacral grooves" or "food-

situated in the direction of the rays, as far as the first axillary joint; and when the arms are numerous, some authors speak of secondary and tertiary radials according to the number of axillaries between the basals and the free arms.

grooves"—which ultimately coalesce to form five primary grooves, which are continued across the ventral surface of the disc to the mouth (fig. 286, A). These ambulacral grooves, in living forms, are ciliated, and along them currents of water are kept up, by which organic particles are conveyed to the mouth. In a number of types, including numerous extinct and a few living forms, the ambulacral furrows are covered in superficially by two, or, more rarely, by four rows of alternating calcareous plates of small size.

The upper or ventral surface of the visceral mass or disc is in all living Crinoids, whether stalked or free, covered with a leathery skin containing calcareous granules or plates, which are sometimes scattered, but sometimes very closely placed; and it exhibits the five principal ambulacral grooves as generally open furrows passing from the bases of the arms to the mouth (fig. 286, A). The mouth itself is central in position, or, rarely, excentric (*Actinometra*), and may be surrounded with five triangular "oral plates," which alternate with the ambulacral grooves. In most *Comatulæ*, the oral plates are present only in the early stages of development (fig. 288), and disappear in the adult; though they are relatively large and well developed in *Thaumatocrinus*. Almost all the Secondary and Tertiary Crinoids resembled the ordinary living forms in the possession of a plated ventral perisome and open ambulacral grooves; and hence such forms have been grouped together by Dr P. H. Carpenter under the name of "Neocrinoids." In all recent Crinoids, further, the upper surface of the body exhibits the aperture of the anus, which is generally excentric, though central in position in some *Actinometræ*, and which is usually placed at the summit of a proboscidiform eminence (fig. 286, A).

On the other hand, in the so-called "Palæocrinoids," embracing under this name all the Crinoids of the Palæozoic rocks, the upper surface of the calyx rarely exhibits open ambulacral grooves, nor is the mouth-opening generally exposed to view. On the contrary, the oral aperture and food-grooves are more or less completely concealed beneath a superficial plated covering, the structure of which varies in different groups. In very many cases, as in the *Actinocrinidæ*, *Platycrinidæ*, *Rhodocrinidæ*, &c., the ventral surface of the calyx is roofed over by a flat or vaulted canopy of calcareous plates, which are firmly united with one another, and completely conceal the subjacent mouth-opening and ambulacral grooves. Five plates which meet in the centre of this vault correspond to the "oral plates" of the Neocrinoids. One of these is larger than the rest, and immediately behind it the vault is perforated by a single, excentric, or, rarely, central aperture, which is often prolonged into a tubular "proboscis," and which is to be regarded as the anus. In all such cases, the ambulacral grooves are continued beneath the above-mentioned

canopy, from the bases of the arms, across the ventral aspect of the calyx, as so many tunnels. During life these lodged both the food-grooves and the water-vessels beneath them, and there is evidence that the latter opened into a circular vessel surrounding the mouth and representing the circular ambulacral vessel of the Echinoderms generally. Hence in specimens of such forms, where the arms have been detached (figs. 294-296), the upper side of the calyx is seen

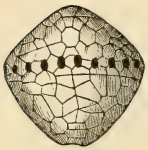

Fig. 294.—Calyx of *Actinocrinus rotundus.*

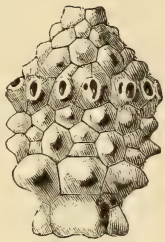

Fig. 295.—Calyx of *Actinocrinus Koninckii.*

Fig. 296.—Calyx of *A. Verneuillanus.* The arms are wanting, and the apertures of the food-grooves at their bases are seen.

to be covered with a plated dome, and the points of insertion of the arms are marked by the openings of the food-grooves on their way inwards to the concealed mouth.

In the great family of the *Cyathocrinidæ*, among the Palæocrinoids, the mouth and convergent food-grooves are concealed from view by a vault which is chiefly composed of the "oral" plates in the centre, together with the united covering-plates of the ambulacra (fig. 297, A). These are all of a much less massive character than in the forms above mentioned, and are readily destroyed. When these tegminal plates have not been preserved—as is very commonly the case—then the upper surface of the calyx (fig. 297, B) exhibits a large central peristomial opening, to which the five ambulacral grooves converge, together with an excentrically placed and often proboscidiform anus. In this family, the peristome is surrounded by five large calyx-interradials, of which one (the "anal plate," fig. 297, *a*) is excavated on one side, and corresponds with the anus. The

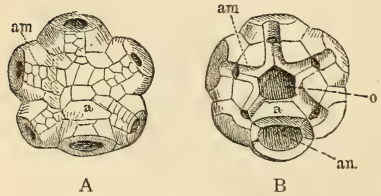

Fig. 297.—Upper surface of the calyx of *Cyathocrinus malvaceus*, showing the superficial plating of the disc preserved (A) and the same removed (B). *am*, Ambulacral grooves, in the one figure roofed in by a double row of minute ossicles, and in the other figure open; *a*, "Anal plate"; *o*, Peristome; *an*, Anus. (After Zittel.)

general structure of the "tegmen calycis" in the great Palæozoic family of the *Poteriocrinidæ* is the same as in the *Cyathocrinidæ*, but both the interradials and the "oral plates" are often inconspicuous, or imperfectly developed. In these forms, also, the excentric anus is prolonged into a proboscidiform tube, which is often of great size (fig. 298).

As regards the *classification* of the Crinoids, the first well-grounded systematic arrangement was that proposed by Johannes Müller, who divided the order into the three sections of the *Tessellata*, the *Articulata*, and the *Costata*. The first of these sections included the Palæozoic Crinoids, and its name was based on the fact that in these the plates of the calyx are united by sutures which do not admit of movement. The section of the *Articulata*, again, included the living, Tertiary, and Secondary Crinoids (*Marsupites* alone excepted), in which the calycine plates are movably articulated; while the section *Costata* comprised only the aberrant Jurassic genus *Saccocoma*. Zittel, in his admirable 'Handbuch der Palæontologie,' has followed Müller's classification, with various emendations and modifications. Müller's classification, though a great advance upon that proposed by his predecessors, cannot be considered, even as modified by Zittel, to be a strictly natural one, since forms which agree in all the other main points of their organisation may differ as regards the mode in which the calycine plates are joined together. Thus the family of the *Ichthyocrinidæ*, though closely resembling the other Palæozoic Crinoids in its essential organisation, is characterised by the possession of movably articulated radial plates, and thus should properly fall under the section of the *Articulata*. The classification which will be here followed is that adopted by Dr P. Herbert Carpenter and by Mr Charles Wachsmuth, in which the *Crinoidea* are divided into the two primary sections of the *Palæocrinoidea* and *Neocrinoidea*. In the division of the *Palæocrinoidea* are comprised all the known Palæozoic Crinoids, and the distinguishing characters of the division are,

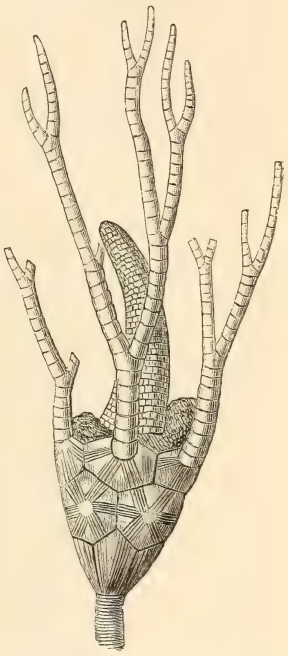

Fig. 298.—Calyx and part of the arms of *Poteriocrinus radiatus*, showing the proboscidiform anal tube. Carboniferous. (After De Koninck and Le Hon.)

roughly speaking, that the calyx is disproportionately large and massively constructed as compared with the arms, interradials being usually present and often united with the radials in such a way as to form a portion of the calyx; while the anal interradius is specially developed, thus rendering the cup unsymmetrical. Moreover, the mouth and food-grooves are generally concealed from view by the development of a more or less definite "vault" above the proper ventral surface of the calyx. On the other hand, the *Neocrinoidea* are all Secondary, Tertiary, or Recent, and are roughly distinguished from the Palæocrinoids by the comparatively small size of the usually symmetrical calyx and the proportionately large development of the arms. The interradials, if present, are rarely incorporated into the calyx, and with one exception (*Thaumatocrinus*) an "anal" interradius cannot be recognised. The higher radial plates are more or less movably articulated, and do not enter into the composition of the calyx. Lastly, the ventral surface of the visceral mass is not covered by a plated dome, but the mouth and ambulacral grooves are exposed to view. Speaking generally, the division *Palæocrinoidea* may be regarded as corresponding with Müller's division of the *Tessellata*, while the section *Neocrinoidea* corresponds with the *Articulata* and *Costata* of the same author.

As regards the *distribution* of the Crinoids *in space*, the order is represented by comparatively few forms in recent seas, and these have mostly a very local range. All the existing forms belong to the division of the Neocrinoids, and the majority of them are referable to the free-living family of the *Comatulidæ*, of which there are not far from two hundred known forms, belonging to six genera (*Antedon*, *Actinometra*, *Atelecrinus*, *Eudiocrinus*, *Promachocrinus*, and *Thaumatocrinus*). On the other hand, there are only about forty known living types of the "Pedunculate" Crinoids, belonging to some half-a-dozen genera (*Pentacrinus*, *Rhizocrinus*, *Bathycrinus*, *Hyocrinus*, *Metacrinus*, and *Holopus*). The *Comatulidæ* have a very wide range in space, being found in almost all seas, but they are essentially inhabitants of shallow water. Many of the living stalked Crinoids, on the other hand, such as *Bathycrinus* and *Hyocrinus*, are only found at great depths in the sea. They do not range, however, below 2500 fathoms, while one species of *Antedon* occurs at a depth of 2900 fathoms.

As regards their *distribution in time*, the entire group of the Palæocrinoids is restricted to the Palæozoic period, and may be said to have attained its maximum development in rocks as ancient as the Silurian. Throughout all Palæozoic time the Crinoids are the predominant types of the Echinoderms, and many of the Ordovician, Silurian, Devonian, and Carboniferous limestones are so extensively

composed of the fragmentary remains of these organisms that they may be properly spoken of as "crinoidal limestones" and "encrinital marbles." The Permian formation (Dyas) is singularly poor in remains of Crinoids, and the commencement of Mesozoic time appears to have been signalised by the complete disappearance of the Palæocrinoids, and the coming in of the Neocrinoids. The first forms of this latter group make their appearance in the Trias (*Encrinus*, &c.), and numerous types are known in the Jurassic and Cretaceous rocks, but the Crinoids no longer play a part of such conspicuous importance as we have seen to have been the case in the Palæozoic period. The earliest forms of the great modern family of the *Comatulidæ* appear in the lower part of the Jurassic system (Middle Lias). The Tertiary formations are by no means rich in Crinoids, and the comparatively limited recent Crinoidal fauna must be regarded as a survival from the earlier part of the Mesozoic period, most of the living types being closely connected with forms which existed at the time when the Triassic and Jurassic deposits were laid down.

In the following synopsis of the families of the *Crinoidea*, the characters and distribution in time of the leading groups will be briefly touched upon, but the less important families can only be defined in the shortest manner possible. The arrangement followed is, in the main, that adopted by Wachsmuth and Springer as regards the Palæocrinoids and by Dr P. Herbert Carpenter as regards the Neocrinoids.

Division A. Palæocrinoidea.

The division of the *Palæocrinoidea* corresponds with Müller's division of the *Tessellata*, as redefined by Zittel, *minus* the two Mesozoic genera *Marsupites* and *Uintacrinus*. The calyx in the Palæocrinoids is comparatively large, with massive plates, and is usually unsymmetrical, the arms being proportionately small. Interradials are usually present, while the anal interradius is specially developed and is readily recognisable. A certain number of the plates above the primary radials are, as a rule, "closely united to one another and to the interradials, so as to form the walls of a relatively large and substantial calyx" (P. H. Carpenter). The ventral surface is covered by a more or less extensive vault, the centre of which is generally occupied by the united oral plates, concealing the mouth and the origins of the ambulacra (fig. 297).

Family 1. *Actinocrinidæ*.—The calyx in this family is always "monocyclic," there being three to five basals, but no "underbasals" (fig. 299). The plates of the cup are firmly united by suture, and the radials take part in the formation of the calyx. Interradial plates are developed, and the lowest "anal" interradial rests directly upon the basals. The arms may be uniserial or biserial

—*i.e.*, they may consist of a single or double row of brachials—but they are most commonly the latter. The ventral surface of the calyx is covered with a vault of heavy plates which are closely connected together. The geological range of the family is from the Ordovician to the Carboniferous inclusive.

The type-genus of this family is *Actinocrinus* itself, in which the calyx, though very variable in shape (figs. 294-296), always possesses three basals, which form a hexagon, and are united superiorly with the five primary radials and the lowest of the anal interradials. There are three cycles of radials, and the highest radials carry each a double series of brachial plates, which support the variously divided arms. There are three or more anal plates, of which the lowest (fig. 299, *a*) always rests upon the basals directly. There is a variable number of interradials, and the column is round. The upper surface of the cup is vaulted over with calcareous plates, and the brachial grooves are continued beneath the vault thus formed, as so many tunnels, to the central and concealed mouth. The anus may or may not be extended into a proboscis, and it is sometimes very excentric, sometimes subcentral. It has been shown that in some of the *Actinocrinidæ* (as in forms belonging to other families) there exists in the interior of the calyx a singular convoluted calcareous plate, of a reticulated texture, shaped somewhat like an ordinary Bubble-shell (*Bulla*), occupying the vertical axis of the body, and often of large size. This has been compared with the calcareous structures present in the "sand-canal" of various Echinoderms; but it is probably rather an extreme development of the discoidal calcareous plates which have been described as strengthening the double wall of the spirally-twisted alimentary canal in the living *Comatulæ*. The genus *Actinocrinus* appears to commence in the Silurian, and is also represented in the Devonian; but it attains its maximum in the Carboniferous, and is wholly unknown in later deposits. *Agaricocrinus* and *Batocrinus* are Carboniferous forms very closely allied to *Actinocrinus*. The Silurian genera *Periechocrinus* and *Megistocrinus* are close allies of *Actinocrinus*, and the Carboniferous *Amphoracrinus* and *Dorycrinus* only differ from it in comparatively trifling particulars.

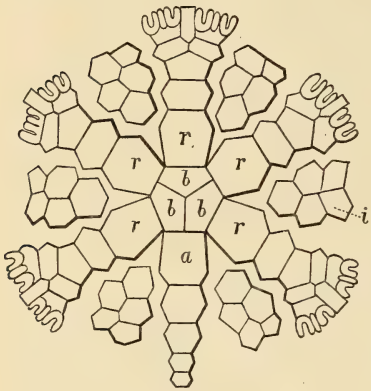

Fig. 299.—Diagram of the dissected calyx of *Actinocrinus* (after Schultze). *b*, Basals; *r*, Radials; *i*, Interradials; *a*, The lowest of the anal plates.

In the Silurian and Devonian genus *Melocrinus*, there are four or three basals, the lowest anal plate is separated from the basals by the primary radials, and the arms are in the form of five free rays giving off lateral armlets. *Melocrinus* is often regarded as the type of the separate family of the *Melocrinidæ*, to which Wachsmuth and Springer also refer the genus *Glyptocrinus*, which will be briefly noticed later.

Among the other genera of the *Actinocrinidæ* may be mentioned *Stelidiocrinus*, *Briarocrinus*, and *Carpocrinus*, which have been regarded as the types of as many families, and all of which are found in the Silurian rocks.

Family 2. *Barrandeocrinidæ*.—This family has been founded by Angelin for the reception of the single genus *Barrandeocrinus*, which occurs in the Silurian rocks of Gotland. In this genus the arms are arranged in pairs, and are reflexed in such a way that their dorsal surfaces rest upon the outer surface of the calyx, while they are at the same time confluent laterally.

Family 3. *Platycrinidæ*. — This family is characterised by the possession of a "monocyclic" calyx, with three, or sometimes two,

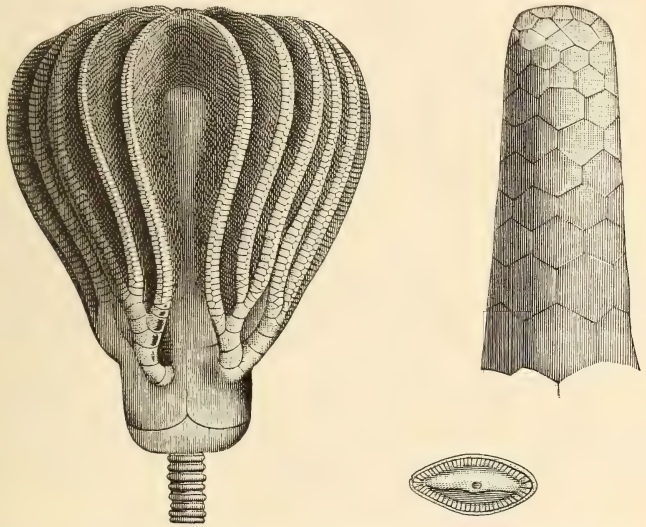

Fig. 300. — *Platycrinus tricontadactylus*. Carboniferous. The left-hand figure shows the calyx, arms, and upper part of the stem, and the figure next this shows the surface of one of the joints of the column. The right-hand figure shows the proboscis.

basals and five radials. There are from three to five plates in each interradial space; but the anal interradials do not come in contact with the basals, except in some forms (*Hexacrinus*). The arms are at least ten in number (fig. 300), and may be uniserial or biserial. The column is round or elliptical, and the neurovascular axial canal is of small size. The geological range of the family is from the Silurian to the Carboniferous inclusive, but the maximum development is attained in the Carboniferous Limestone.

The type-genus of the *Platycrinidæ* is *Platycrinus* itself, in which the cup is composed of three basals and a single cycle of radials, amongst

which the anal interradial is not intercalated. The succeeding radials are embraced in the free arms, and do not form part of the calyx. The arms are numerous and bifurcated, and all the divisions carry pinnules. There are three or five interradials in each of the interradial spaces, and there may be one large, or three small anal plates. The column is rounded near the calyx, but its lower joints are oval and compressed. There is, typically, a large anal proboscis. In connection with the proboscis of *Platycrinus*, we may just notice the well-known fact that in many specimens (as is the case with other Crinoids possessing a similar elongated anal tube) there is found in close apposition with the proboscis, and often placed upon its actual summit, the shell of a fossil Univalve (apparently almost always, or always, a species of *Platyceras*). It was originally supposed that the Crinoid had been fossilised in the act of eating the Mollusc—the anal tube being regarded as the mouth—but all the living Crinoids feed upon microscopic animalcules, and this supposition is therefore, *prima facie*, an improbable one. It has also been shown by Meek and Worthen that the *Platyceras* must have lived for a long time attached to the proboscis of the Crinoid, since the lip of its shell has closely adapted its form to that of the surface to which it is attached. We may therefore safely accept the conclusion reached by these observers, that the *Platyceras* was in the habit of attaching itself parasitically to the side or summit of the proboscis of *Platycrinus* and other Crinoids, thus obtaining a share of the minute animalcules upon which its host lived.

The genus *Platycrinus*, as defined by Wachsmuth and Springer, is almost entirely confined to the Carboniferous period, being represented by many species in the Carboniferous Limestone. One or two small forms, however, occur in the Devonian. The genus *Hexacrinus* is closely allied to *Platycrinus*, but it possesses a large anal plate, which rests directly upon the basals (as in *Actinocrinus*). The genus is strictly Devonian, and the species are mostly European.

By Wachsmuth and Springer the genus *Hexacrinus* is regarded, probably correctly, as the type of the distinct family of the *Hexacrinidæ*, to which they also refer *Hystricrinus* and *Dichocrinus*. Of the remaining genera of the *Platycrinidæ*, the only one which needs special mention is the somewhat aberrant Ordovician and Devonian genus *Coccocrinus*. In this genus, the vault is entirely formed by five large oral plates, which rest upon the interradials and conceal the mouth.

Family 4. *Rhodocrinidæ*.—The forms included in this family have a dicyclic calyx (fig. 292), but the underbasals may be very small, and are sometimes completely concealed from external view (*Glyptocrinus*). The underbasals are usually five in number, sometimes three: and there are five basals. Interradials are well developed, but the anal interradius is "scarcely distinct" (Wachsmuth and Springer). A very characteristic feature, however, is that the first radials are separated by interradials which rest upon the basals. The arms may be uniserial or biserial. The species of this family range from the Ordovician to the Carboniferous inclusive.

The type-genus of this family is *Rhodocrinus* itself, which ranges from the Silurian to the Carboniferous. The underbasals in this genus (fig. 292) are five in number, and are well developed. The five lowest interradials

rest upon the basals, and form with the first radials a ring of ten plates; while the arms, varying in number from ten to twenty, are bifurcated two or three times during their course. Allied to *Rhodocrinus* is the genus *Ollacrinus* (*Gilbertsocrinus*) of the Carboniferous Limestone.

The genus *Glyptocrinus* has been commonly referred to the *Rhodocrinidæ*, but it is now placed by Wachsmuth and Springer in the *Melocrinidæ*, while other authorities regard it as the type of a separate family (*Glyptocrinidæ*). In this genus, the turbinate calyx possesses underbasals, but these are of small size, and may be quite rudimentary. The calycine

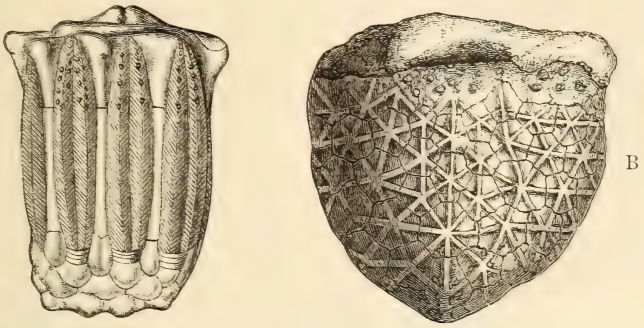

Fig. 301.—A, Calyx and arms of *Eucalyptocrinus rosaceus*, viewed from one side, of the natural size—Devonian (after Schultze); B, Calyx of *Glyptocrinus basalis*, viewed from one side, of the natural size—Ordovician (after M'Coy).

plates are ornamented with characteristic radiating ridges (fig. 301, B); the arms are uniserial; and the column is annulated or moniliform. All the species of *Glyptocrinus* appear to belong to the Ordovician period.

Family 5. *Calyptocrinidæ*.—In the remarkable forms included in this family, the calyx is regular and "monocyclic," flattened or hollowed out basally, and passing superiorly into a flask-shaped tegmen, which is narrowed above, and terminates in a centrally placed anal aperture surrounded by regularly arranged polygonal plates. The arms are, typically, twenty in number, biserial, and not projecting beyond the level of the upper limit of the calyx; and they are situated between riblike processes of the upper margin of the cup, or in special lateral niches formed by vertical outgrowths from the wall of the calyx. The members of this family are exclusively confined to the Silurian and Devonian formations, the principal genus being *Eucalyptocrinus*.

In *Eucalyptocrinus* (fig. 301, A), the calyx is inverted upon itself, the calycine cup being deeply concave at its base, so as to look like the bottom of a wine-bottle. Within this basal funnel are situated the four small basals, which are succeeded by five large primary radials. These are strongly bent, one-half of each passing up into the basal funnel, while the other half appears on the lower and lateral aspects of the cup. Two other rows of radials succeed these, the tertiary radials being unusually large, and each supporting the bases of two arms. The interradial

plates are developed in a most singular manner, so as to form a series of five linear, clavate processes, which separate and support the arms; five other precisely similar processes being borne by the axillary radials. The arms thus come to lie in deep grooves or niches in the sides of the calice, the upper surface of which they do not reach. The upper surface is completely vaulted over, and is mainly formed by the upper ends of the ten interbrachial processes just spoken of, in the centre of which is a small circular anal aperture, surrounded by five or more plates. The species of *Eucalyptocrinus* are found in the Silurian and Devonian rocks; and the Silurian genus *Hypanthocrinus* differs principally from the preceding in the fact that the base of the calyx is not funnel-shaped. The Silurian genus *Corymbocrinus* (fig. 302) has been likewise placed in the neighbourhood of *Eucalyptocrinus*, but is now considered by Wachsmuth and Springer as belonging rather to the family of the *Actinocrinidæ*. In this genus the calyx resembles that of *Eucalyptocrinus* in having a deep funnel-shaped depression at its base, but the arms are long and much divided. Lastly, the genus *Callicrinus*, also Silurian, is in most structural features closely allied to *Eucalyptocrinus*, and appears to represent an earlier phase in the development of the family.

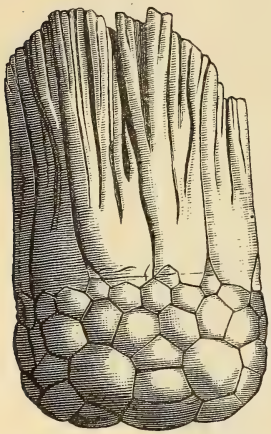

Fig. 302. — Calyx and arms of *Corymbocrinus polydactylus*. Wenlock Limestone of Britain. (After M'Coy.)

Family 6. *Crotalocrinidæ*.—In this small and remarkable family, the calyx is "dicyclic," with small underbasals and large basals. The arms are uniserial, without pinnæ, but furnished with numerous

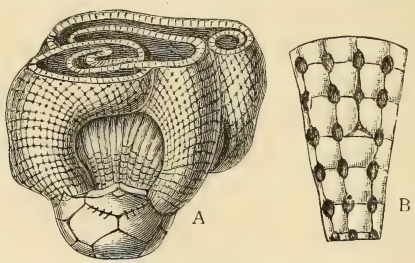

Fig. 303.—A, Calyx and arms of *Crotalocrinus Loveni*, cut across to show how the arms are rolled up; B, A portion of the network formed by the arms, enlarged. Silurian. (After J. Müller.)

branches, by the coalescence of which they become more or less extensively connected with one another laterally, generally forming wide, inrolled, foliaceous expansions. The anus, so far as known, has the form of an excentric, proboscidiform, plated tube. The

centre of the vault is occupied by five oral plates, while the ambulacral grooves of the arms and their lateral branches are covered in by small calcareous plates. The genera of this family are Silurian, but *Cleiocrinus*, if rightly referred here, is Ordovician.

The type-genus of this family is *Crotalocrinus* (*Anthocrinus*), one of the most beautiful Crinoids of the Wenlock Limestone of Gotland and Britain. The calyx consists of five small underbasals and five large basals, with a single zone of radials, while interradials are wanting, with the exception of a single small anal plate. The arms are bifurcated, and the subdivisions unite with one another by means of lateral processes, thus giving rise to a network, perforated by numerous apertures (fig. 303). The Silurian genus *Enallocrinus* is nearly allied to *Crotalocrinus*, but the arms become free towards their extremities.

Family 7. *Ichthyocrinidæ*.—In this family the calyx is "dicyclic," but the three underbasals are small, and are mostly not visible externally. The radials articulate upon one another, and are united laterally by the perisomic plates of the disc. The arms are short, bifurcating, and often in contact laterally, thus forming an upward continuation of the calyx (fig. 304, A); while pinnules are apparently wanting. The disc had open ambulacral grooves, and was covered with perisomic plates, like that of a recent Crinoid. Its central part was occupied by five oral plates, which in some species, if not in all, were separate from one another, so as to open the mouth to the exterior. The members of this family are found in the Silurian, Devonian, and Carboniferous deposits.

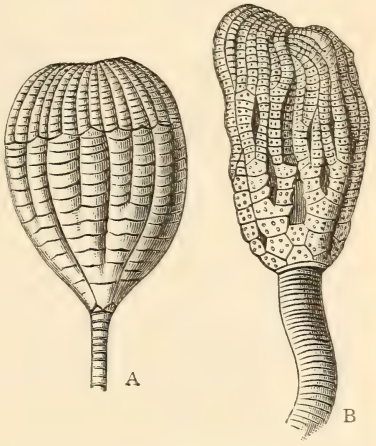

Fig. 304.—A, Side-view of the calyx of *Ichthyocrinus lævis*, from the Silurian (Niagara Limestone) of North America; B, Calyx and upper part of the column of *Taxocrinus tuberculatus*, from the Silurian (Wenlock Limestone) of Britain. (After Hall and M'Coy.)

The typical genera of the *Ichthyocrinidæ*—such as *Ichthyocrinus* itself (Silurian to Carboniferous), *Lecanocrinus* (Silurian and Devonian), and *Mespilocrinus* (Carboniferous)—are characterised generally by the imperfect separation of the calyx and arms, the latter being commonly in close apposition laterally (fig. 304, A). On the other hand, the genus *Taxocrinus* (fig. 304, B) represents a section of the family—sometimes raised to the rank of a separate family (*Taxocrinidæ*)—in which the arms are well developed and repeatedly bifurcated. The species of *Taxocrinus* are found in the Silurian, Devonian, and Carboniferous

rocks; and the genus *Forbesiocrinus*, with a similar geological range, is principally distinguished from this by the more abundant development of the interradial plates.

Family 8. *Haplocrinidæ*.—In this family the calyx is small and spheroidal, and is composed of basals and radials, underbasals being absent. The ventral surface of the calyx exhibits five large "oral" plates, forming a low pyramid, which is excavated along the sutures of the plates to receive the bases of the arms (fig. 305). There is no definite anal plate, but the anal opening perforates one of the oral plates, which is somewhat larger than its fellows. The arms are poorly developed. The family, as defined by Wachsmuth and Springer, includes only the two genera *Haplocrinus* (fig. 305) and *Allagecrinus*, of which the former is mainly if not wholly Devonian in its range, while the latter is exclusively confined to the

Fig. 305.—*Haplocrinus mespiliformis*. The calyx viewed from below, from one side, and from above, and enlarged. Devonian.

Carboniferous rocks. Both genera comprise very small Crinoids, which are in some respects simpler in their construction than the normal members of the order, and may be considered as permanently representing the larval condition of the Palæocrinoids. *Allagecrinus* is remarkable for the inequality in the size of its radials, some of which may be axillary and bear two arms. For this reason it is regarded by some authors as the type of a distinct family.

Family 9. *Symbathocrinidæ*.—In this family the calyx is small, and is composed of basals and radials only. The central portion of the ventral surface of the calyx exhibits a circle of oral plates. The arms are uniserial, exceedingly long, and folded together. The principal genera of this family are *Symbathocrinus* (Devonian and Carboniferous), *Pisocrinus* (Silurian), and *Triacrinus* (Devonian and Carboniferous).

Family 10. *Cupressocrinidæ*.—In this family the large, basin-shaped calyx is apparently of the "dicyclic" type, the underbasals being anchylosed to form a solid disc, which some authors regard as being an enlarged top stem-joint, in which case the calyx would be "monocyclic." Upon this disc rest five basals, followed by five radials, the upper edges of which are truncated and form a

horizontal line. Reposing directly upon the radials are the five first brachials, which are as wide as the radials, but are of very small vertical thickness. The arms are massive, moving as in one piece, uniserial, and undivided. They gradually diminish towards their apices, and by the accurate apposition of their edges together, form a pentagonal pyramid. The arm-plates bear numerous small and incurved pinnules, six or more on either side of each joint. These roof in the deep ambulacral grooves, which seem also to have had a definite calcareous skeleton of their own. Between the bases of the arms, in the interior of the cup, is placed a so-called "consolidating apparatus," formed of five laterally anchylosed calcareous pieces, which apparently really represent "the united muscle-plates of the radials" (P. H. Carpenter). This peculiar apparatus covers the greater part of the ventral surface of the calyx, and the mouth appears to have been placed in its centre. The column is obtusely quadrangular, annulated, and traversed by a large central canal surrounded by four smaller tubes.

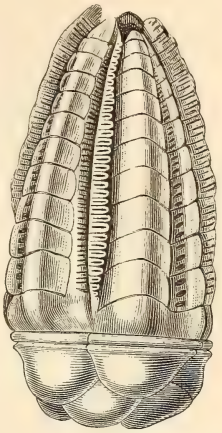

Fig. 306.—Side-view of the cup of *Cupressocrinus crassus*, with the arms folded up, of the natural size. Devonian. (After Schultze.)

The only genus of this family is *Cupressocrinus* itself, the species of which are exclusively Devonian, and appear to have been wholly confined to the European area. The characters of the genus need not be more fully discussed, the principal ones having been mentioned in the diagnosis of the family.

Family 11. *Gasterocomidæ*.—In this family the calyx (fig. 307) is small and spheroidal, and is typically dicyclic, the underbasals

Fig. 307.—*Gasterocoma antiqua*, from the Devonian rocks of the Eifel, enlarged twice. *a*, The calyx viewed from the side; *b*, The anal aspect of the calyx; *c*, The ventral surface of the calyx. (After Schultze—copied from Zittel.)

being usually represented by a simple pentagonal plate. This plate may, however, be merely an enlarged top stem-joint (as in *Cupressocrinus*), and Zittel regards *Nanocrinus* as being monocyclic. There are five basals, and generally an equal number of radials, with one

or more interradials in the anal interradius. In *Nanocrinus*, however, there are only four arm-bearing radials, one of which is axillary. In the type-genus *Gasterocoma*, one of the basals is notched for the anal opening, which is situated between it and the first anal plate. The arms are recumbent or widely divergent, and the stem is generally four-sided, and is perforated by four canals, surrounding, or confluent with, a larger central canal. The two principal genera of this family are *Gasterocoma* (*Epactocrinus*) and *Nanocrinus*, both of which are found in the Devonian deposits of Europe.

Family 12. *Hybocrinidæ*.—The members of this small family exhibit embryonic characters, and have a "monocyclic" base, with imperfectly developed radials, and a very small ventral sac. The basals are five in number, and are very large. The arms are simple and without pinnules; and one or more of them may be undeveloped, or only represented by recurrent ambulacra which run over the outer surface of the calyx. The genera included by Wachsmuth and Springer in this family are *Hybocrinus*, *Hybocystites*, *Hoplocrinus*, and *Baerocrinus*, all of which are confined to the Ordovician rocks.

Family 13. *Heterocrinidæ*.—In this family are comprised Palæocrinoids with a relatively large ventral and small dorsal development of the calyx. The basis, as in the preceding family, is "monocyclic," thus differing from that of the *Cyathocrinidæ* and *Poteriocrinidæ*, in which underbasals are present. The arms are much more developed than in the *Hybocrinidæ*, and are furnished with long pinnules. The principal genera are *Heterocrinus* and *Stenocrinus*, both of which are found in the Ordovician rocks of North America.

Family 14. *Anomalocrinidæ*.—In this family the only genus is *Anomalocrinus*, the species of which are found in the Ordovician rocks of North America. The calyx in this genus is large and depressed, with a "monocyclic" basis. The pinnules of the arms are not given off alternately from opposite sides (as in Crinoids generally), "but from every successive joint on one side at a time, from one bifurcation to the next, where they change on both rami to the opposite" (Wachsmuth and Springer).

Family 15. *Belemnocrinidæ*.—The only genus included in this family is the *Belemnocrinus* of the Carboniferous Limestone of North America. In this genus, the basis is "monocyclic," with no underbasals, but with relatively large basals. The ventral side of the calyx is well developed, but the visceral cavity is extremely small. There is an anal plate placed in a line with the radials. The anal proboscis is large and porous. Lastly, the pinnules of the arms are given off regularly at every second or third joint, and not alternately from all the brachials. According to Wachsmuth and Springer, the

genus forms a connecting-link between the *Heterocrinidæ* and the *Cyathocrinidæ*.

Family 16. *Cyathocrinidæ*.—In this important family of Crinoids, the calyx is irregular, and is of the "dicyclic" type, consisting of five underbasals (fig. 308, *b*), five basals (*p*), five primary radials (*r*), and from one to three anal interradials (*a*). The ventral surface of the calyx is mainly formed by the large interradial plates, between which are the ambulacral grooves, roofed over with small calcareous plates (fig. 297). The arms are uniserial, long, repeatedly bifurcated

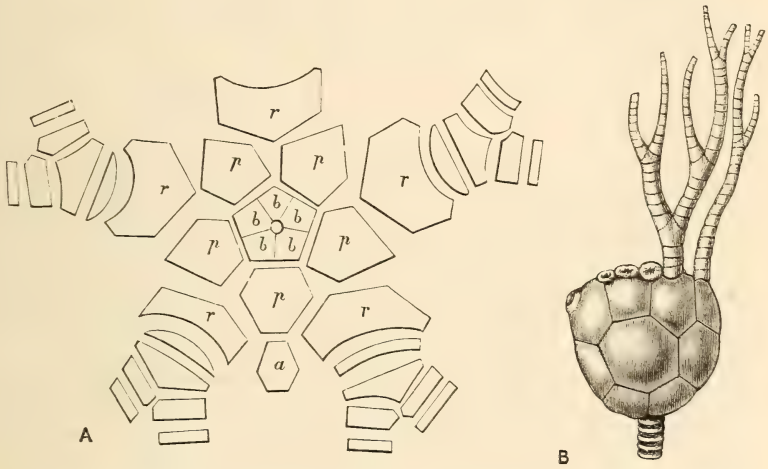

Fig. 308.—A, Diagram, showing the dissected calyx of *Barycrinus* (after Hall): *b*, Underbasals; *p*, Basals; *r*, Lowest of the three radials ("primary radials"); *a*, Anal plate. B, Calyx and part of the arms of *Cyathocrinus planus*, of the natural size. Carboniferous.

(fig. 309), and without true pinnules. The family of the *Cyathocrinidæ* is closely allied to that of the *Poteriocrinidæ*, but the arm-joints are differently articulated in the two, and the arms are repeatedly bifurcated in the former group; whereas in the latter the arms may remain simple after the first bifurcation, or branch irregularly, and they, further, carry pinnules. The range of the *Cyathocrinidæ* in time is from the Silurian to the Permian inclusive.

The principal genus in this family is *Cyathocrinus* itself (fig. 309), which ranges from the Silurian to the Permian, but attains its maximum development in the Carboniferous Limestone. In this genus the calyx is small and basin-shaped, with long, frequently divided arms. The ventral side is slightly convex, and a plated anal tube is present. The column is round, and is composed of very narrow articulations, which are perforated by a five-angled neurovascular canal. *Barycrinus*, of the Carboniferous rocks of North America, is nearly related in most respects to *Cyathocrinus*; while *Dendrocrinus* (Ordovician), *Carabo-*

crinus (Ordovician), and *Homocrinus* (Silurian and Devonian) are other leading genera of this family.

Family 17. *Poteriocrinidæ.*—In this family the calyx is "dicyclic," and is essentially similar to that of *Cyathocrinus*, consisting of five underbasals, five basals, five primary radials, and from one to five interradials (fig. 291). The arms are simple or bifurcated, and carry long pinnules. The ventral surface of the calyx is elevated and convex, and a greatly developed anal tube or proboscis is usually present (fig. 298). The genera of this family appear to be principally, if not wholly, confined to the Devonian and Carboniferous rocks, by far the larger number of forms belonging to the latter.

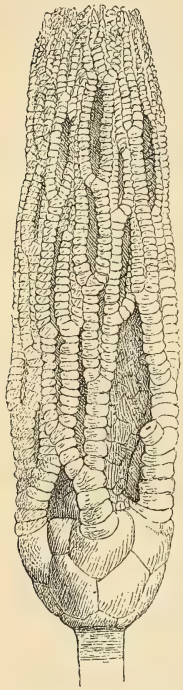

Fig. 309.—Side-view of the calyx and arms of *Cyathocrinus longimanus*, of the natural size, Silurian. (After Angelin — copied from Zittel.)

The principal genus of this family is *Poteriocrinus* itself (fig. 298), which is closely allied to *Cyathocrinus*, from which it is distinguished principally by the more elevated form of the ventral sac, the great development of the anal tube, and the structure of the arms. These latter organs may be simple or branched, but in either case are provided with pinnules, while the radials are truncated superiorly, where they articulate with the brachials. On the other hand, in *Cyathocrinus* the arms are without pinnules, and the first radials (fig. 308, *r*) articulate with the second by means of horse-shoe-shaped facets. The species of *Poteriocrinus* are mainly Carboniferous, but a few forms are known from the Devonian rocks. Closely allied genera are *Zeacrinus* (Carboniferous) and *Scaphiocrinus* (Carboniferous and Devonian).

Family 18. *Astylocrinidæ.*—The calyx in this family is *free*, the peduncle of the larva being evanescent; and it is composed of firmly united massive plates (fig. 310). Typically, the calyx is "dicyclic," but *Edriocrinus*, if rightly referred here, has no underbasals. There are two cycles of radials, the second of which is axillary, and the arms are provided with long pinnules. Anal interradial plates are developed, and the dorsal side of the calyx does not carry cirri. The type-genus of this family is *Agassizocrinus* (= *Astylocrinus*), which is found in the Carboniferous Limestone of North America. The genus *Edriocrinus*, from the Silurian rocks of North America, has also been provisionally placed in this family by Wachsmuth and Springer.

In *Agassizocrinus* (figs. 310, 311) the calyx was attached in its early condition by a larval peduncle, but the adult was free. The underbasals

become united to form an almost solid disc, which is slightly hollowed above, and exhibits a group of pits, which probably lodged extensions of the "chambered organ." The Silurian genus *Edriocrinus* was also free in its adult condition, but underbasals are wanting, and it possesses other peculiarities as well.

Family 19. *Catillocrinidæ*.—In this small family, the calyx is of small size and of the "monocyclic" type. The radials are remarkably unequal in point of size, two of them being greatly developed, and forming the larger part of the margin of the calyx. These carry a much larger number of the arms than the three small radials. The arms are simple, uniserial, and long, and the column is round.

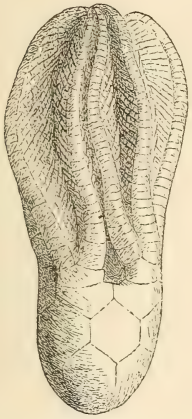

Fig. 310.—Side-view of a complete example of *Agassizocrinus dactyliformis* (=*Astylocrinus lævis*, F. Roemer). Carboniferous, North America. (After Meek and Worthen.)

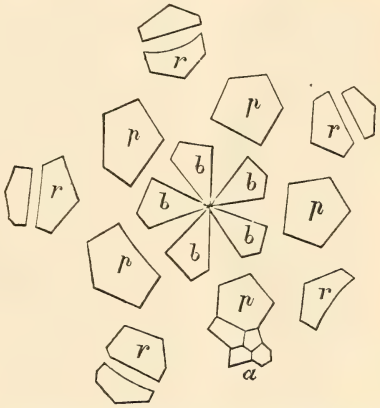

Fig. 311.—Dissected calyx of *Agassizocrinus*. *b*, Underbasals; *p*, Basals; *r*, Radials; *a*, Anal plates. (After Hall.)

The type-genus is *Catillocrinus*, the geological horizon of which is the Carboniferous rocks of North America.

Family 20. *Calceocrinidæ* (= *Cheirocrinidæ*).—This family includes only the aberrant genus *Calceocrinus* (= *Cheirocrinus*), which ranges from the Ordovician to the Carboniferous. In this genus the small and irregular calyx, with its crown of arms, is fixed in such a way as to hang downwards from the summit of the column. The calyx is "monocyclic," and there are only three basals, which, in the natural position of the cup, are situated posteriorly. The radials are of unequal size, only three of them bearing arms. The basals and radials are united by ligaments and muscles, so that a distinct articulation is formed at this point in the cup. The arms are bifurcated, and those on the posterior side are the strongest.

Division B. Neocrinoidea.

This division of the *Crinoidea* corresponds with the *Articulata* of Müller (with the addition of the genera *Marsupites* and *Uintacrinus*), together with the *Costata* of the same author. As defined by Dr P. Herbert Carpenter, the forms included in the *Neocrinoidea* possess a relatively minute, usually symmetrical, regularly pentamerous calyx, the arms being in general greatly developed. There are, as a rule, five equal and similar basals, and five also equal and similar radials. Underbasals are rarely present (*Encrinus*, *Extracrinus*, and *Marsupites*). Interradials are rarely developed, and, when present, no special "anal" interradius (except in *Thaumatocrinus* alone) is recognisable. The higher radials do not enter largely into the composition of the calyx, and are usually more or less movable, being generally united to the succeeding plates by a muscular articulation. The ventral surface of the calyx is not concealed by an external canopy or vault of calcareous plates, but the aperture of the mouth, with the ambulacral grooves converging to it, is exposed to view. The ambulacral grooves may be more or less roofed in by calcareous plates, and "oral" plates, when present, "may be limited to larval existence, or remain through life partially covering the peristome, but capable of being separated so as to open the mouth to the exterior" (P. H. Carpenter). All the Neocrinoids are Secondary, Tertiary, or Recent, no Palæozoic representatives of the division being at present known.

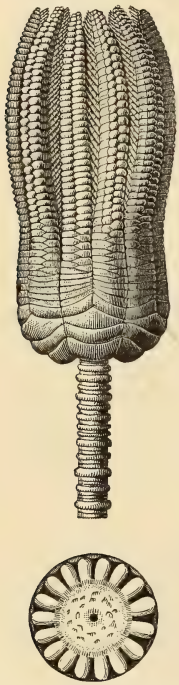

Fig. 312. — *Encrinus liliiformis*. Muschelkalk. The lower figure shows the articulating surface of one of the column-joints.

Family 1. *Encrinidæ*.—In this family the calyx is shallow and basin-shaped, with a "dicyclic" basis. There are five underbasals, which are of very small size, and are concealed by the uppermost joint of the column. These are succeeded by five large basals, followed in turn by five radials, the whole of these plates being firmly united by suture. The primary radials are followed by two others, the second of which is axillary and bears two arms, which sometimes fork again, so that there are ten, or, rarely, twenty divisions in all. The arms (fig. 312) are often biserial, are abundantly furnished with pinnules, and form by their apposition a kind of pyramid. The upper column-joints (fig. 312) are generally alternately large and small. The joint-surfaces are furnished with

radial ridges, and each exhibits in the centre a small round or pentagonal neurovascular canal (see the lower figure in fig. 312). Lastly, the visceral mass was enclosed in a plated perisome essentially similar to that of the recent Crinoids.

The only clearly established genus belonging to this family is *Encrinus* itself, all the species of which are Triassic. A well-known species of this genus is the Lily-encrinite (*E. liliiformis*, fig. 312), the heads of which are not very rare in some localities in the Muschelkalk of Germany.

Family 2. *Eugeniacrinidæ*.—In this singular family, the calyx (fig. 313) is apparently composed only of primary radial plates, which rest directly upon the enlarged uppermost joint of the column. Basals have not been detected, but it is probable that they were present in a rudimentary form. There are two additional rows of radials, which bear ten uniserial arms, and the base of the column is expanded, and serves to cement the animal to foreign bodies. The geological range of the family is restricted to the Jurassic and Cretaceous rocks.

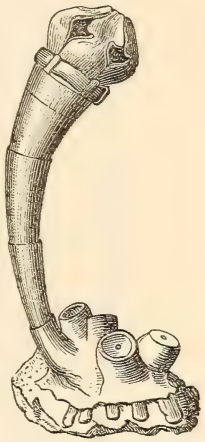

Fig. 313.—*Eugeniacrinus caryophyllatus*, without the arms, restored. Jurassic rocks. (After Fraas—copied from Zittel.)

The principal genus of this family is *Eugeniacrinus* itself (fig. 313), which occurs in the Jurassic and Cretaceous deposits of Europe. The column-joints and clove-shaped calyx of species of this genus are not uncommon, but the arms have never been found attached to the cup, and no example of a complete calyx has yet been detected.

Family 3. *Holopidæ*.—In this aberrant family the calyx is without a column, and is firmly adherent to foreign bodies by the under surface of the wide cup. The basals are fused with one another, and usually with the radials also, in which latter case the presence of distinct basals can only be inferred. The arms (where known) are thick, massive, and spirally inrolled.

In the recent genus *Holopus* the basals and radials are "completely anchylosed into an asymmetrical tube-like calyx, which is fixed by an irregularly expanded base" (P. H. Carpenter). Allied to this extraordinary living type are a few fossil forms from the Mesozoic and later Tertiary deposits. Of these the genera *Cotylecrinus* (*Cotylederma*) and *Eudesicrinus* are confined to the Lias; while *Cyathidium* is found in the late Cretaceous deposits (Faxoe Limestone) and in the Eocene Tertiary.

Family 4. *Hyocrinidæ*.—This family includes only the living

genus *Hyocrinus*, which is in some respects related to the Palæocrinoids. In this genus the calyx-plates are thin, and the cup consists of both basals and radials, the former being only three in number. The radials are five in number, and each carries a single undivided arm. The arm-joints are united by "syzygy" into groups of two or three, the terminal joint of each group bearing a long pinnule. There are five large "oral" plates round the mouth. The stem consists of short cylindrical joints, the articular surfaces of which are simple or slightly striated.

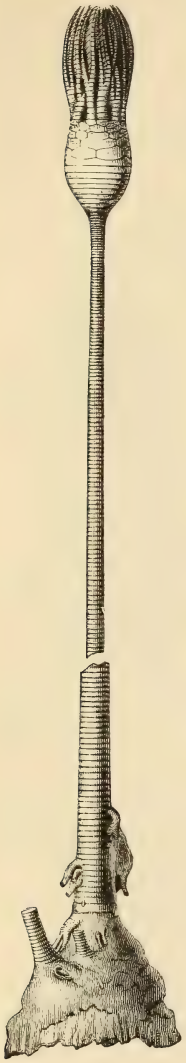

Fig. 314.—*Apiocrinus Roissyanus*. Middle Oolite (Jurassic).

Family 5. *Plicatocrinidæ*. — This family includes only the Jurassic genus *Plicatocrinus*, which is considered by Zittel as nearly allied to, or identical with, *Hyocrinus*. Basal plates are, however, said to be absent; while the arms are short, and the joints are not united by "syzygy," and are provided with short pinnules.

Family 6. *Apiocrinidæ*.—In this family the calyx is regular, and the upper stem-joints are, typically, wider than those below, the upper part of the column thus passing gradually into the base of the cup. The basals are five in number, and are surmounted by three cycles of radials, each cycle being normally pentamerous. The stem is expanded at its base for attachment to foreign bodies, or is furnished with branching roots or cirri (fig. 314), and the apposed faces of its component joints are marked with radial striæ. The earliest types of this family (*Apiocrinus* and *Millericrinus*) appear in the Jurassic rocks, and became extinct in the Lower Cretaceous period.

In the genus *Apiocrinus*, comprising the so-called "Pear-encrinites," there is a long cylindrical stem, rooted to foreign bodies by an expanded base (fig. 314). The upper joints of the stem are narrower, as regards vertical height, than the lower ones, while they are widened out laterally, so as to pass gradually into the massive pyriform cup. The uppermost joint of the stem is much enlarged, and carries the five basals, which are in turn succeeded by three rows of radials. The species of *Apiocrinus* are found in the Jurassic and Lower Cretaceous rocks. In the genus *Millericrinus*, with a very similar geological range, the upper stem-joints are only

very gradually widened out, and the top one is not very greatly larger than those below it.

Family 7. *Bourgueticrinidæ.*—In this family the calyx is very simple, consisting of five basals and five radials. The stem-joints are dice-box-shaped, their faces bearing transverse ridges with fossæ at their sides which lodge the interarticular ligaments. The stem is attached below by a branching root or by radicular cirri, and there are five or ten slender arms, the joints of which are united in pairs, with a pinnule on the distal joint of each pair only. The disc bears five oral plates of variable size, and the brachial ambulacra have two rows of covering-plates.

This family differs essentially from the *Apiocrinidæ* in the relatively small size of the calycular cavity and in the more or less dice-box-shaped character of the stem-joints. In the type-genus *Bourgueticrinus* there is a small pyriform calyx, passing gradually downwards into the thickened upper part of the stem, the top joints of which are much enlarged, while it is fixed below by a root-like prolongation. *Bourgueticrinus* is essentially a Cretaceous genus, but has been described as occurring both in Jurassic and in Tertiary strata, solely, however, on the very uncertain evidence afforded by stem-joints. The family is represented by two living genera. *Bathycrinus* ranges from 1000 to 2400 fathoms in the Atlantic, but is not yet known in the fossil state; while *Rhizocrinus*, which occurs at smaller depths, ranges back to the Eocene Tertiary. In the former type the basals are small and firmly united, while the radials are long and comparatively free, and there are ten arms. On the other hand, *Rhizocrinus* has long basals and short, closely united radials, as in *Bourgueticrinus;* while there are but five arms, the joints of which are united by "syzygy," only the upper joint of each pair bearing a pinnule. In both genera the upper stem-joints are thin and discoidal, while the ambulacral furrows of the arms and pinnules are protected by delicate calcareous plates. The disc of *Rhizocrinus* is, further, covered by large "oral" plates, which are much reduced or absent in *Bathycrinus.*

Family 8. *Pentacrinidæ.*—This family is defined by Dr P. H. Carpenter as comprising forms in which the calyx is small relatively to the stem and arms, and is "composed of five basals and five radials, with underbasals in one genus. The rays divide from one to eight times. The stem bears verticils of cirri at intervals. Two joints are united by syzygy at each node, to the upper one of which the cirri are articulated. The internodes are traversed by five ligamentous bundles, which are interradially disposed, and give rise to a more or less petaloid figure on the joint-faces. No root nor radicular cirri." The range of the family is from the Trias to the present day.

The type-genus of this family is *Pentacrinus* itself, which has the geological range of the family. In this well-known genus (fig. 289) the joint-faces of the pentagonal stem are marked by crenated ridges

arranged in a floriform manner, each petaloid sector having from five to eight large teeth at the sides. There are only three radials, and the arms rarely divide more than thrice. The genus *Metacrinus*, only known by living forms, differs from *Pentacrinus* chiefly in the possession of from four to six radials, the characters of the joint-faces being the same in both genera. Lastly, the Mesozoic genus *Extracrinus* (fig. 290) is separated from *Pentacrinus* by the possession of a ring of underbasals, and by the much more frequent subdivision of the arms. The faces of the stem-joints in this genus are also different, the petaloid sectors being linear, and having delicately crenulated edges. In all three genera the visceral mass is surrounded by a plated perisome, which unites the lower part of the rays and arms.

Family 9. *Marsupitidæ*.—This family comprises *free* Crinoids, in which the larval peduncle is lost in the adult. A "centrodorsal" plate is present, but this does not bear cirri. The calyx may be monocyclic or dicyclic, and there are no definite interradial plates. The only genera included in this family are *Marsupites* and *Uintacrinus*, both of which are confined to the Cretaceous period.

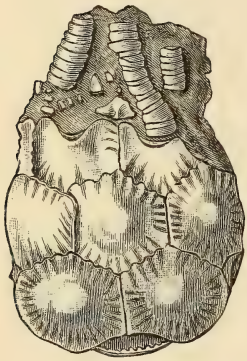

Fig. 315.—Side-view of the calyx and bases of the arms of *Marsupites ornatus*, from the Chalk.

The genus *Marsupites* comprises the so-called "Tortoise-encrinites" of the Chalk, and is characterised by the possession of a globular calyx, composed of large thin plates, carrying bifurcated uniserial arms. The calyx is dicyclic, the underbasals, five in number, surrounding a central pentagonal plate, which has usually been regarded as an enlarged top stem-joint ("centrodorsal"). There is, however, reason to think that it is rather homologous with the suranal plate of *Salenia*, and therefore a "dorsocentral" plate. There are five basals and three rows of radials, but regular interradials are not developed. The ventral surface of the calyx is vaulted, and covered with small calcareous plates; and the anus is sub-central. The genus *Uintacrinus* resembles *Marsupites* in its general form, and in the possession of a pentagonal "centrodorsal" (?) which does not carry cirri. On the other hand, the globular calyx is monocyclic, and there are ten arms, the bases of which are united laterally by numerous perisomic plates, as in the *Pentacrinidæ*.

Family 10. *Comatulidæ*.—This family of Crinoids comprises the "Feather-stars," all of which (except *Thiollericrinus*) lose the larval peduncle, and are therefore free in the adult condition (fig. 284). The base of the calyx is closed by a "centrodorsal" plate (fig. 285, *cd*), which represents the enlarged top stem-joint, and upon which jointed cirri are developed. The calyx is apparently "monocyclic," but underbasals have recently been discovered in the larva

of the Rosy Feather-star, and there are grounds for believing that their presence is characteristic of the family. They never reach any great size, however, and fuse at an early period with the enlarged top stem-joint or "centrodorsal." The basals are very generally rudimentary, being reduced to a small "rosette-plate," concealed between the centrodorsal and the primary radials. In *Atelecrinus* and *Thaumatocrinus*, however, and in most fossil *Comatulæ*, the basals persist and are visible externally. There are three, or, rarely, two cycles of radials; and, except in *Thaumatocrinus*, definite calyx-interradials are not developed. There are five or ten arms, which are either simple or more or less divided. A large number of living forms of the "*Comatulæ*" are known, with a very wide range in space. As regards their distribution in time, the earliest types of the Feather-stars are found in the Jurassic

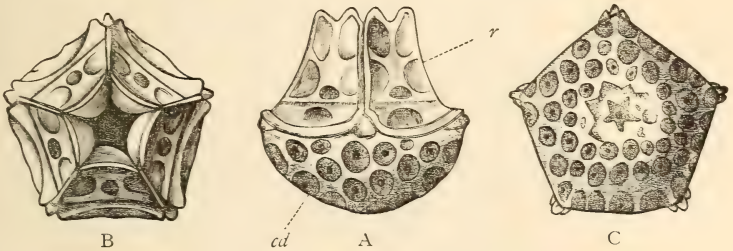

Fig. 316.—Centrodorsal (*cd*) and radial pentagon (*r*) of *Antedon incurva*, enlarged six times. Cretaceous (Upper Greensand). A, Side-view; B, View from above; C, View from below. (After P. H. Carpenter.)

rocks (*Antedon*, *Actinometra*, &c.), and there are also various Cretaceous and Tertiary types. The parts most commonly preserved in a fossil condition are the centrodorsal plate and radial pentagon (fig. 316); and upon remains of this nature, before their true character was understood, the generic name of *Solanocrinus* ("*Glenotremites*") was founded. The names of *Allionia*, *Ganymeda*, &c., were also based upon the isolated centrodorsals of fossil *Comatulæ*.

The extensive genus *Antedon* possesses a central or subcentral mouth and ten or more arms, while the basals of the recent species form a "rosette," and are invisible externally. The earliest fossil species appear in the Lias. *Eudiocrinus* resembles *Antedon*, but has only five arms. The genus is represented by a single Cretaceous form, but living types are known. *Actinometra* differs from *Antedon* in the fact that the mouth is excentric or marginal in position. The genus ranges from the Jurassic period to the present day. Lastly, in the Jurassic and Cretaceous genus *Thiollericrinus*, the centrodorsal plate exhibits a cavity which is usually filled by the first joint of the persistent stem, the lower

joints of which are dice-box-shaped. The genus has therefore been compared to an *Antedon* with a *Bourgueticrinus* stem.

Family 11. *Saccocomidæ*.—This remarkable family comprises only the single genus *Saccocoma*, which is represented by one species (*S. pectinata*, fig. 317) only, from the Upper Jurassic rocks (Litho-

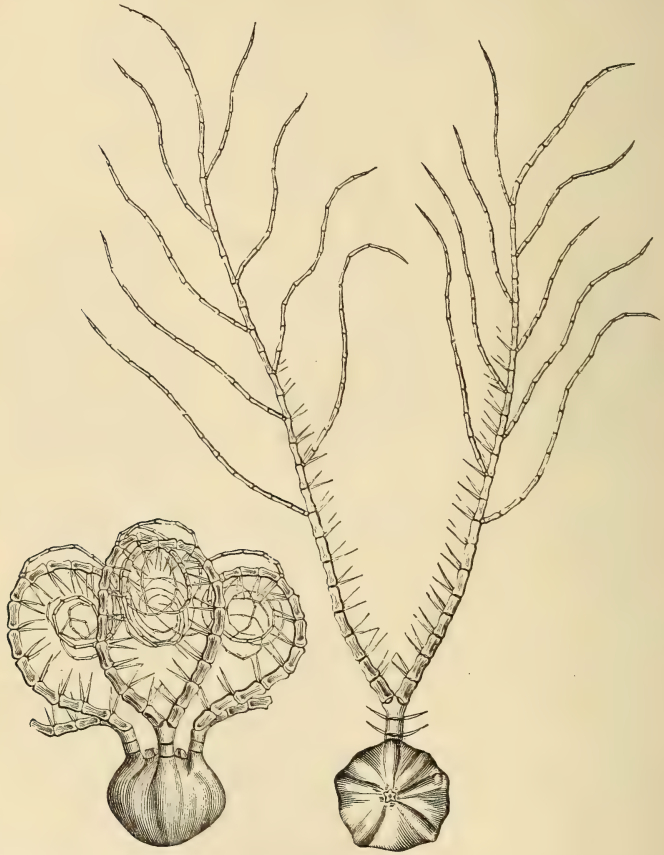

Fig. 317.—*Saccocoma pectinata*, from the Upper Jurassic of Bavaria. The left-hand figure shows the complete organism, with the arms inrolled.

graphic Slates) of Bavaria. In this singular genus, the organism is free, the larval peduncle being evanescent. The calyx is composed of a single minute basal supporting a cycle of five, thin, closely united radials, ornamented externally with ten radiating ribs, and the ventral surface is occupied by five oral plates. There are

five arms, which bifurcate once, and have the power of rolling up. The arms carry a few long pinnules like those of *Hyocrinus*, and possess small undivided spine-like processes. The skeletal tissue is throughout peculiar in not being dense, but in having a tolerably loose reticulated structure. The characters of *Saccocoma* are so peculiar, that the genus was placed by Müller in a separate division of Crinoids, to which he applied the name of *Costata*.

APPENDIX.

Since the preceding pages were written, some important discoveries have been made respecting the nature of the ventral covering in *Encrinus* and *Taxocrinus*, the latter genus having a plated disc exactly like that of a Neocrinoid, with open ambulacra and an exposed mouth surrounded by five oral plates. There can be little doubt that the other *Ichthyocrinidæ* were essentially in the same condition: while *Encrinus* proves to be very closely allied to the Carboniferous *Poteriocrinidæ*, such as *Erisocrinus* and *Stemmatocrinus*.

Under these circumstances, it is no longer possible to regard the *Neocrinoidea* and *Palæocrinoidea* as well-defined primary groups, though the names may be conveniently retained as expressing a general stratigraphical distinction between the older and the younger Crinoids. Messrs Wachsmuth and Springer have already suggested the outlines of a new classification which, with slight modification by Dr P. H. Carpenter—to whom the author is indebted for the present note—will probably result in something like the following scheme.

Order I. Coadunata.

Crinoids in which the interradials, where present, are incorporated into the calyx, the latter generally also including the higher radials, which are immovably united by suture; while an anal system is well developed. The mouth and ambulacra are subtegminal, the centre of the vault being occupied by five oral plates, and the arms are usually biserial.

Sub-order I. Camerata.

Families—Actinocrinidæ, Rhodocrinidæ, Reteocrinidæ, Glyptocrinidæ, Melocrinidæ, Platycrinidæ, Hexacrinidæ, Barrandeocrinidæ, Calyptocrinidæ.

Sub-order II. Reticulata.

Family—Crotalocrinidæ.

Order II. Inadunata.

Crinoids in which the arms are free from the first radials. The calyx generally has an anal side, and frequently a dicyclic base. Interradials may or may not be present. The mouth may be concealed beneath an oral pyramid, or in the centre of a plated disc with open ambulacra.

Sub-order I. Larviformia.—Interradial and anal plates rarely present. Base monocyclic: arms uniserial. Ambulacra closed, and mouth concealed by an oral pyramid.

Families—Haplocrinidæ, Symbathocrinidæ, Cupressocrinidæ, Gasterocomidæ.

Sub-order II. Fistulata.—Interradial and anal plates generally well developed. Base usually dicyclic, and arms often biserial. Oral plates generally reduced, and the calyx covered by a plated perisome which often bears open ambulacra. The posterior interradius may be greatly developed to form the ventral sac or anal proboscis.

Families — Hybocrinidæ, Heterocrinidæ, Anomalocrinidæ, Belemnocrinidæ, Cyathocrinidæ, Poteriocrinidæ, Encrinidæ, Astylocrinidæ, Catillocrinidæ, Calceocrinidæ.

Order III. Articulata.

Crinoids in which the higher radials are more or less movably articulated on one another, though often united laterally by the plated perisome of the disc. The ambulacra are generally open and the mouth exposed, though often surrounded by oral plates. Interradial and anal plates rarely present: arms uniserial.

Sub-order I. Impinnata.

Family—Ichthyocrinidæ.

Sub-order II. Pinnata.

Families—Pentacrinidæ, Comatulidæ, Apiocrinidæ, Bourgueticrinidæ, Eugeniacrinidæ, Holopidæ, Marsupitidæ, Plicatocrinidæ, Hyocrinidæ, Saccocomidæ.

CHAPTER XXVI.

PELMATOZOA—continued.

CYSTOIDEA AND BLASTOIDEA.

Class II. Cystoidea.

The Cystideans are an extinct group of Echinoderms in which *the body (or "calyx") is spherical or ovate, and is enclosed in a case composed of more or fewer calcareous plates, which are usually united by suture but irregularly arranged, and do not exhibit perfect radial symmetry. The plates of the calyx are in general pierced by more or less numerous pores, which probably communicated with internal organs, and which may be regarded as almost certainly connected with the function of respiration. A jointed column may be present or absent.*

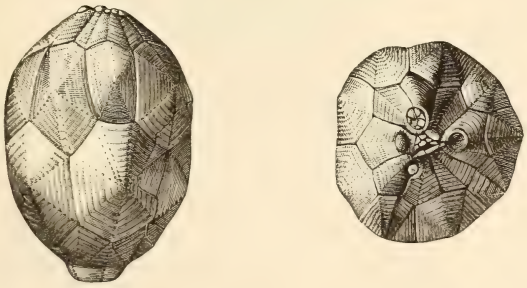

Fig. 318.—*Hemiscosmites pyriformis*, one of the Cystideans. The right-hand figure shows the upper surface of the calyx.

The upper surface of the calyx usually shows radiating ambulacral grooves, a central oral aperture, and a lateral anal (?) *opening, with sometimes a small ovarian* (?) *opening. Arms are imperfectly developed, or may be wanting.*

In general form the Cystideans are globular, oval, pear-shaped,

conical, or subcylindrical, and they generally resemble the Crinoids in consisting of a stem or "column" and a body or "calyx." The stem is sometimes long (as in *Caryocrinus*); but it is usually feebly developed, and often attenuated towards its base, sometimes terminating in a single long spindle-shaped piece (*Lepadocrinus*, fig. 326, D), in which case it probably did not serve as an organ of attachment. In other cases the stem is rudimentary (as in *Echinosphærites*) or it may be even absent altogether, the organism being then mostly attached to foreign objects by the base of the calyx, or, rarely, free.

The calyx is composed of a number of polygonal plates, which usually exhibit no marked radial disposition, though they are sometimes of limited number and arranged according to a definite plan. In other cases the calyx-plates are indefinite in number and arrangement; and in some forms the number and arrangement of the plates may be definite on one side of the calyx and indefinite

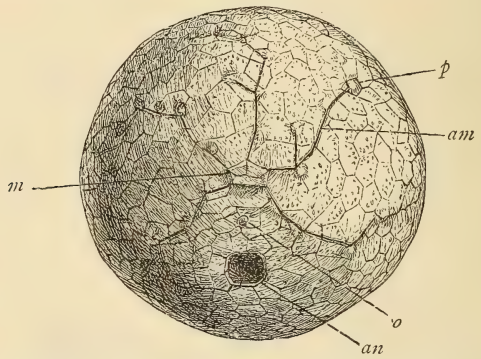

Fig. 319.—Upper surface of the calyx of *Glyptosphærites Leuchtenbergi*, from the Ordovician rocks of Russia. *m*, Mouth, covered by the oral plates; *am*, Ambulacral grooves; *p*, Socket for one of the armlets; *an*, Anus, without its covering-plates; *o*, Supposed ovarian aperture.

on the other. The base of the calyx is usually readily recognised by the presence of the articular surface for the top joint of the stem, or by being fixed to some foreign object; and the upper surface generally shows two or three openings, the nature and functions of which have been much disputed. One of these openings is central or subcentral in position (319, *m*), and is often protected in well-preserved specimens with a covering of five small plates, representing the orals of the Crinoids, while it forms the point of convergence of from two to five, simple or branched grooves which run over the ventral surface of the calyx (*am*). These grooves clearly correspond to the "ambulacral grooves" or "food-grooves" of the Crinoids, and there can therefore be no doubt that the aperture in

question is the mouth. A second aperture (fig. 319, *an*) is placed excentrically, usually on the upper surface of the calyx, and in good specimens is furnished with five or six triangular calcareous plates, which are arranged to form a sort of cone or "valvular pyramid," and which serve for the closure of the opening. It is not necessary to discuss the various views which have been put forward as to the functions of this orifice, but there is every reason to believe that it is really the anus. In many cases there is a third opening, which is always of small size and always placed near the mouth (fig. 319, *o*). This aperture has been commonly regarded as being of the nature of an "ovarian" aperture or genital pore.

In well-preserved examples, the upper surface of the calyx commonly exhibits simple or branched grooves (fig. 319, *am*), which radiate from the mouth, and obviously are of the nature of "ambulacral grooves" or "food-grooves." In some cases, as, for example, in *Callocystites* (fig. 320) and in *Lepadocrinus* (fig. 326, c), the ambulacral groove is bordered on each side with a row of delicate jointed pinnulæ, which are also grooved on their ventral faces. In such cases, the ambulacral grooves may be looked upon as representing recumbent arms which have become soldered down to the surface of the calyx. In cases where the ambulacral groove is bordered by a single row of pinnules, the arm may be supposed to be fastened down to the calyx by one of its sides instead of by the dorsal surface. In other Cystideans the upper surface of the calyx exhibits irregularly scattered articular facets, which, in the perfect condition, served for the attachment of small unbranched jointed filaments. These may be regarded as of the nature of "armlets" or simple arms, rather than as pinnulæ. They are seen in such genera as *Glyptosphærites* (fig. 319, *p*), *Caryocrinus* (fig. 326, A), and *Pleurocystites* (fig. 326, B), and they can be sometimes shown to possess a ventral groove, which is provided with small calcareous covering-plates. Lastly, in the genus *Comarocystites* there are four free arms, which differ from the structures just spoken of, and agree with the arms of the Crinoids generally, in being provided with lateral pinnæ.

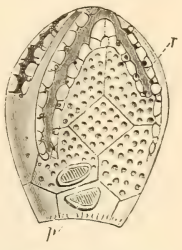

Fig. 320.—Side-view of the calyx of *Callocystites Jewettii*, from the Silurian of North America, showing the ambulacral grooves (*r*) and the origins of the pinnules on the sides of these. *p*, Pore-rhombs. (After Hall.)

In some forms of the Cystideans (*Cryptocrinus*, *Malocystites*, &c.) the plates of the calyx appear to be completely imperforate. In the majority of cases, however, the walls of the calyx are more or less extensively perforated by pores or fissures, which usually open directly on the outer surface of the body, but are in other cases

closed by an exceedingly thin calcareous membrane, while they invariably traverse the entire thickness of the plates. Their arrangement differs much in different types of the Cystideans, and they afford therefore important evidence in classification. In certain forms (such as *Glyptosphærites*, *Gomphocystites*, &c.) the pores are conjugate, or are united in pairs, the individual plates possessing

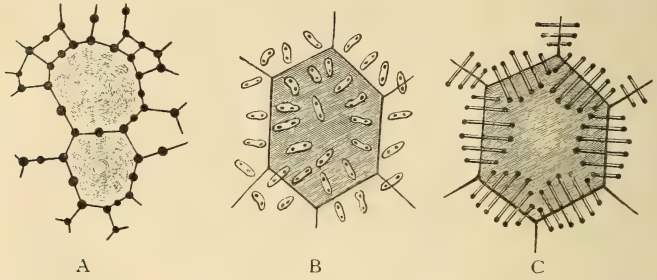

Fig. 321.—A, Part of the calyx of *Eocystites? longidactylus*, from the Cambrian rocks of North America, enlarged, showing pores passing between adjoining plates; B, Plate of *Glyptosphærites Leuchtenbergi*, enlarged, showing double pores; C, Plate of *Echinosphærites aurantium*, showing diffused pore-rhombs, enlarged, from the Ordovician rocks of Russia. (A is after Walcott.)

several of such pairs (fig. 321, B). In other forms, the pores are arranged in rows, a row on one plate being united by grooves or fissures, sometimes on the exterior of the calyx or at other times on its interior, with a corresponding row on an adjoining plate. These rows of connected pores (fig. 322) are arranged so as to form lozenge-shaped or rhombic figures; in such a manner that one-half of

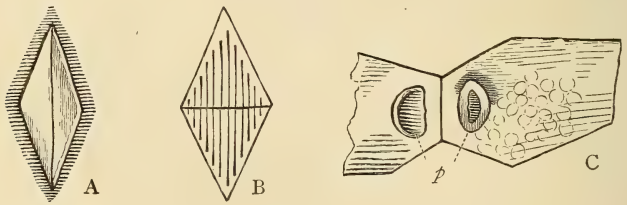

Fig. 322.—A, Pore-rhomb of *Glyptocystites multiporus* (Billings); B, Pore-rhomb of *Pleurocystites* (Billings); C, Two plates of *Callocystites Jewettii* (Hall), showing the pore-rhombs (*p*). All enlarged.

each rhomb belongs to one plate and the other half to its contiguous neighbour, while the grooves connecting the two component rows of pores pass across the line of suture between the two plates, either externally or internally. In some types, as in *Echinosphærites* (fig. 321, C) and *Caryocystites*, these "pore-rhombs" are very numerous, and are present upon nearly all the plates of the calyx. In other

cases (as in *Caryocrinus* and *Hemicosmites*) they are only developed on the side-walls of the calyx, and are absent from its upper surface. In other cases, again, as in *Pleurocystites* (fig. 326, B) or *Callocystites* (fig. 322, C), the pore-rhombs, or "pectinated rhombs," as they have been often termed, are comparatively few in number, and their component halves not only stand on contiguous plates, but may be separated externally by an interval.

It would seem extremely probable that the differences in the form and arrangement of the pores in different groups of Cystideans, which have been pointed out above, are really an indication of a fundamental difference in the nature and function of these structures. In those Cystideans which possess "pore-rhombs" (*Rhombiferi*), there seems no reason to doubt that these structures were connected with internally-placed, folded tubes similar to the "hydrospires" of the Blastoids, and that they acted as respiratory organs. On the other hand, it has been suggested by Lovén, with much probability, that the linked pores of *Glyptosphærites* and its allies (*Diploporitidæ*) were connected with the ambulacral system, and that, like the pores in the test of the Urchins, they were occupied by pedicels. On this view, "hydrospires" are wanting in the types in question, and the function of respiration would be discharged by the tube-feet. If this suggestion be accepted, the Diploporous Cystoids would be comparable to the Sporadiporous Holothurians or to such Urchins as *Melonites*. They would, however, differ from the Urchins generally in the want of definite radial symmetry in the plates of the test, and also in the fact that the pores for the tube-feet perforate the plates of the *interambulacral* areas, instead of being confined to the ambulacral areas only.[1] The Cystoids (*Aporitidæ*) in which neither pores nor "pore-rhombs" are developed, occupy a dubious position from a systematic point of view. They differ widely from the preceding groups in some respects, and it is possible that they may ultimately find a place elsewhere.

As regards their *distribution in time*, the Cystideans are not only wholly extinct, but they are entirely restricted to the Palæozoic period, ranging from the Cambrian period to the Carboniferous Limestone, but attaining their maximum of development in deposits of Ordovician age. The few Cambrian forms which have hitherto been detected are only known from imperfect examples, and their precise structure is incompletely understood. Upon such remains have been founded several genera (*Eocystites*, *Trochocystites*, *Protocystites*, &c.), but these do not at present admit of precise definition.

[1] In such Urchins as *Scutella* (fig. 240) the branches of the ambulacral grooves on the actinal surface extend into the interambulacral regions, and are lined by minute tube-feet, while in *Echinanthus* there are isolated "locomotive" pores scattered over many of the interambulacral plates.

In one of these ancient types, from the Cambrian rocks of North America, which Mr Walcott has doubtfully referred to the genus *Eocystites*, there appears to be the exceptional character that the pores are formed by the apposition of corresponding indentations in the edges of contiguous plates (fig. 321, A). In the Ordovician series, and particularly in strata of Llandeilo-Bala age, the remains of Cystideans are sometimes abundant, and the group attains here its maximum. In the Silurian period Cystideans are less abundant, and in the Devonian formation only very few forms (*Tiaracrinus*, *Ateleocystites*, *Strobilocystites*, &c.) are known to occur. Lastly, if *Codaster* be removed to the Blastoids, the group of the Cystideans is chiefly represented in Carboniferous deposits by the aberrant genus *Agelacrinus*.

As regards their *classification*, the Cystideans may be conveniently divided into the three orders of the *Aporitidæ*, *Diploporitidæ*, and *Rhombiferi*, according as the calycine plates are imperforate, are pierced by yoked pairs of pores indiscriminately distributed, or have their pores arranged in "pore-rhombs"; and the characters and principal genera of these three groups may be very briefly glanced at here.

Order 1. Aporitidæ.—In this group are comprised all those Cystideans in which the calyx-plates are destitute of pores. Of the genera of this group *Cryptocrinus* (fig. 325, B) has a globular calyx, composed of comparatively few plates arranged in a tolerably definite manner, there being three basals, succeeded by two cycles of pentagonal plates. The central mouth is, in perfect specimens, covered by a vault of small calcareous plates, and the laterally placed anus is provided with a "valvular pyramid." The stem and arms are unknown, and the genus is confined to the Ordovician rocks. *Malocystites*, from the Ordovician deposits of Canada, possesses an indefinite number of plates in the calyx, and the mouth is excentric, and is surrounded by radiating ambulacral furrows. In *Anomalocystites* (=*Ateleocystites*, Billings) the calyx is also composed of an indefinite number of plates, which are ornamented with transverse striæ. One side of the calyx is convex, while the other is flat or concave, and the summit is provided with delicate armlets or pinnulæ. The species of this genus range from the Ordovician to the Devonian. The most remarkable type of the imperforate Cystideans, however, is that presented by *Agelacrinus* and *Edrioaster*, which have sometimes been regarded as constituting a special family (*Agelacrinidæ*). In the genus *Agelacrinus* (including *Hemicystites*, Hall) the body (fig. 323, A) is in the form of a depressed or convex disc, attached by the whole of its under surface to some foreign body, and therefore devoid of a peduncle. The upper or ventral surface of the disc is covered with numerous

small calcareous plates, which may or may not overlap in an imbricating manner, and exhibits in its centre the opening of the mouth, protected by four "oral" plates. Radiating from the mouth are five curved ambulacral grooves, and in one of the interradial spaces is situated the opening of the anus (*o*), protected by a "pyramid" of calcareous plates. The species of *Agelacrinus* are found in the Ordovician, Silurian, Devonian, and Carboniferous rocks. The genus *Edrioaster* (fig. 323, B), from the Ordovician rocks, agrees in most of its general characters with *Agelacrinus*, but the ambulacral grooves are furnished with a double row of pores on each side.

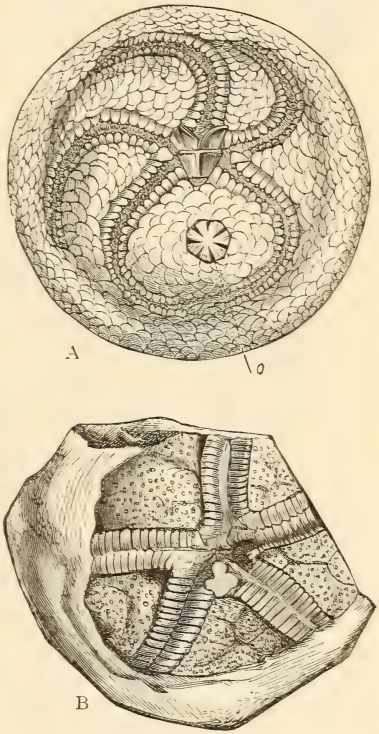

Fig. 323.—A, Upper surface of *Agelacrinus Cincinnatiensis*, enlarged two and a half diameters. Ordovician (after Hall). B, Upper surface of an imperfect specimen of *Edrioaster Bigsbyi*, of the natural size. Ordovician (after Billings). *o*, Anal aperture.

Order 2. Diploporitidæ.—In the Cystideans which are included in this group, the pores are linked or united in pairs, and the individual calyx-plates are pierced by several of such pairs (fig. 321, B). There is, as before pointed out, much probability in the view put forth by Lovén, that the yoked pores of the *Diploporitidæ* served for the passage of tube-feet, and that they thus differ in their real nature from the "pore-rhombs" of the Rhombiferous Cystoids. If this view be correct, the present group is very sharply separated from both the other groups of Cystoids.

As the type of the *Diploporitidæ*, the Ordovician genus *Glyptosphærites* may be taken, in which the globular calyx (fig. 319) is composed of numerous polygonal plates, each of which is perforated by a larger or smaller number of conjugate pores. The mouth is central, and is covered by five oral plates, while converging to it are five branching ambulacral grooves, at the terminations of which are the articular facets to which the armlets or pinnulæ were attached. On one side is the comparatively large opening of the anus, and between the two is a small

aperture which has been usually regarded as a genital pore. The calyx was furnished with a stem composed of thin annular joints. The genus *Sphæronites*, also Ordovician in its range, is allied to the preceding in several points, but there was no stem, and the calyx was adherent by its base to foreign bodies. In the Silurian genus *Gomphocystites* (fig. 324) the calyx has a very peculiar shape, being pyriform, very narrow below, and inflated at its summit. The calyx-plates are in numerous cycles, and have superficial granules, along with yoked pores. The mouth is central, and is surrounded by five spirally wound ambulacral grooves. In *Holocystites*, again, the calyx (fig. 325, F) is long and subcylindrical, and is composed of six or more ranges of hexagonal or polygonal plates. The mouth is central, and the calyx was furnished with a short stem, or was sessile. The genus is found in the Silurian rocks of North America and Europe.

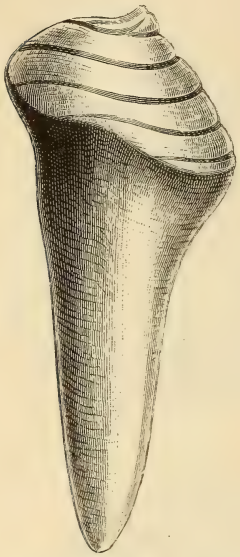

Fig. 324.—Side-view of the cast of the calyx of *Gomphocystites glans*, of the natural size, from the Silurian (Niagara Limestone) of North America. (After Hall.)

Order 3. Rhombiferi.—The Cystideans included in this order are characterised by the possession of pores arranged in rows, corresponding rows in adjoining plates being connected, externally or internally, by grooves or slits which cross the lines of suture between the plates. The pores are thus arranged in groups, which are usually more or less lozenge-shaped, and which are known as "pore-rhombs." The pore-rhombs were probably connected internally with organs similar to those which will be described in dealing with the Blastoids as "hydrospires," and their function seems to have been certainly respiratory.

In one section of this order the plates are indefinite in number, and the pore-rhombs are distributed indifferently over the whole calyx, and are exceedingly numerous. A good example of this section is the well-known Ordovician genus *Echinosphærites* (fig. 325, A), in which the calyx is of large size, globular, and stemless, its base being attached to foreign bodies. The calyx-plates are very numerous, polygonal, with pore-rhombs on every side (fig. 321, C). At the apex is the mouth, and the anus is lateral and is protected by a large "valvular pyramid," while a small ovarian (?) opening is placed between the two. *Caryocystites*, also Ordovician, is nearly

related to *Echinosphærites*, but the calyx is more of an ovoidal form, and the plates are ridged or striated. Allied genera are *Palæocystites* and *Comarocystites*, both from the Ordovician rocks of North America, and the latter remarkable in having a small number of pinnate arms.

In a second group of the *Rhombiferi*, the pore-rhombs are confined to the sides of the calyx, and the upper surface is formed of imperforate plates, while the arrangement of the calycine plates

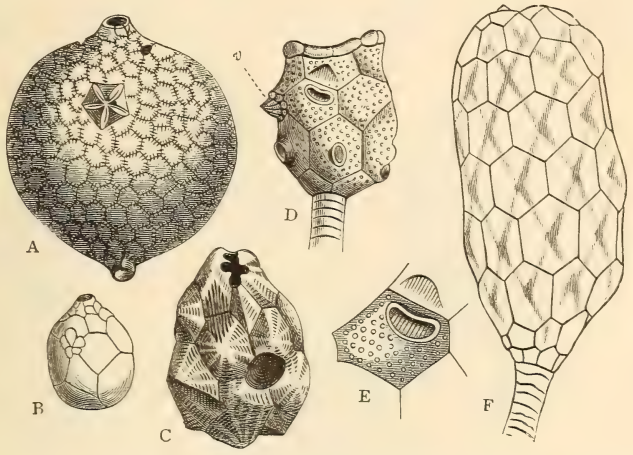

Fig. 325.—A, *Echinosphærites aurantium*; B, *Cryptocrinus lævis*; C, *Echinoencrinus Senkenbergi*; D, *Echinoencrinus* (?) *armatus*; E, One of the "pectinated rhombs" of the last, enlarged; F, *Holocystites cylindricus*. *v*, Valvular anal pyramid. All the specimens are viewed from one side. (A, B, and C are after von Buch; D is after Edward Forbes; and F is after Hall.)

generally is to a greater or less extent radial. A good example of this group is afforded by the genus *Caryocrinus* (fig. 326, A), which is widely distributed in the Silurian rocks of North America. In this genus there is a long and cylindrical column, which carries an ovoid calyx, the upper surface of which exhibits the articular facets to which free-jointed armlets or pinnulæ were attached. The lateral calyx-plates show externally lines of pores radiating from their centres, and an internal examination shows that these pores are connected by canals into pairs, so as to form a series of "rhombs." *Hemicosmites* (fig. 318) is an allied genus, which is found in the Ordovician and Silurian deposits of Europe.

Finally, in a third group of the *Rhombiferi* are included forms in which the calyx-plates are generally more or less definite in number, and more or less clearly arranged in a quinary manner, while the "pore-rhombs" are limited in number, and are often so disposed that

the component halves of each are separated externally by an interval (fig. 322, c). Of the more important genera of this group, *Pleurocystites* is remarkable in having the perisomatic plates on the dorsal side of the calyx large and definitely arranged, while those of the ventral side are numerous and indefinite. The summit of the calyx carries two jointed armlets (fig. 326, b), and there are three "pore-rhombs," or, as these structures were termed by Edward Forbes, "pectinated rhombs." The genus is found in the Ordovician rocks of Canada. In the Ordovician genus *Echinoencrinus* (fig. 325, c) the calyx is composed of four series of plates, there being four basals,

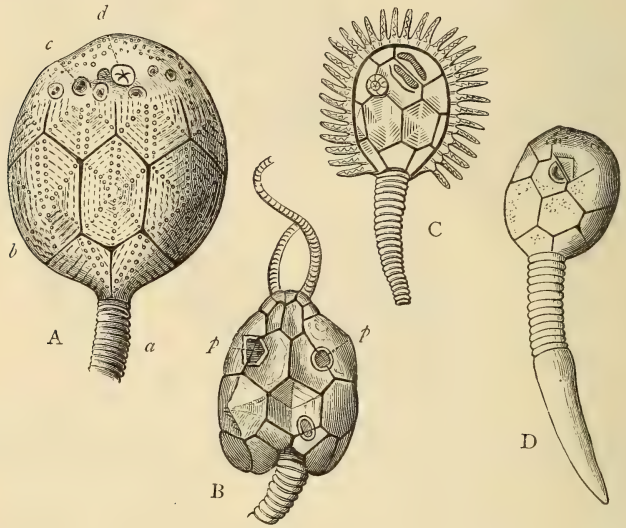

Fig. 326.—A, *Caryocrinus ornatus: a*, Column; *b*, Calyx; *c*, Scars where pinnulæ were attached; *d*, Valvular pyramid. B, *Pleurocystites squamosus* (dorsal side): *p p*, Two of the pore-rhombs. C, *Lepadocrinus* (*Pseudocrinus*) *bifasciatus*. D, *Lepadocrinus Gebhardi*.

and five plates in every cycle above this. There are three "pectinated rhombs," and the anal opening is of large size and is placed on one side. The Silurian Cystideans referred to this genus by Edward Forbes under the names of *E. baccatus* and *E. armatus* (fig. 325, d) differ in some important points from the type of *Echinoencrinus*. *Glyptocystites*, of the Ordovician rocks of America and Europe, is allied to the preceding, but possesses numerous "pore-rhombs" (ten to twelve in number), no other genus of this section having more than three or four of these organs. In *Lepadocrinus*—with which Zittel unites *Pseudocrinus* and *Apiocystites*—the calyx is ovoid, more or less quadrangular, with a long stem, which becomes attenuated

below, or ends in an elongated and pointed ossicle (fig. 326, D). The mouth is central, and there are two or four ambulacral grooves, which in well-preserved examples are bordered by short pinnules (fig. 326, C). The anus is excentric, and is furnished with valvular plates, and there are three reniform or triangular pore-rhombs. The genus is principally Silurian. Lastly, in *Callocystites*, as in the preceding genus, the calyx consists of four zones of plates, of which the lowest consists of four basals. The mouth is central, and there are five ambulacral grooves (fig. 320), which are bordered by well-developed pinnules. The anus is excentric, and there are four pectinated rhombs. The species of *Callocystites* are found in the Silurian rocks of North America.

Class III. Blastoidea.

This class includes extinct Echinoderms in which *the body* ("*calyx*") *is pyriform, clavate, ovate, or globular, and is attached by a short jointed peduncle, which is in some cases wanting. The calyx exhibits complete radial symmetry, and is enclosed in a covering of suturally united calcareous plates, consisting of basals, radials, and interradials. The upper surface exhibits five ambulacral areas, usually of a more or less petaloid shape, which radiate from the mouth, the latter being superior and central, and being concealed by a covering of small calcareous plates, some of which represent the "orals" of the Crinoids, while the ambulacral grooves are protected by a double row of "covering-plates." Small jointed appendages or "pinnules" are attached, in a single or double row, to the sides of the ambulacral fields, but no true arms are present. "Hydrospires," opening by five or ten apertures round the mouth or by interradial fissures, are present, but are limited to the radial and interradial plates, never extending on to the basals.*

The Blastoids form a peculiar group of Palæozoic Echinoderms, in which the body is generally supported by means of a short peduncle composed of discoidal joints, though in some cases no stem appears to have been present. The calyx is globular, ovoid, clavate, or bell-shaped, and is remarkable for its regular radial symmetry. Underbasals, such as are found in the "dicyclic" Crinoids, are not developed, but the calycine plates consist of a cycle of basals, a row of radials, and a circle of interradial ("deltoid") plates. The basals (fig. 327, A and 328, B) are three in number, two being comparatively large and of equal size, while the third is much smaller. Following the basals is a cycle of five "radials," which are usually of large size, and form the sides of the calyx (figs. 327 and 328, *d*). The radials have been sometimes spoken of as the "forked plates," owing to the fact that each is deeply divided or

incised distally, in such a way that the two arms of the plate enclose the lower end of one of the ambulacral fields. The radials differ from the corresponding plates of the Crinoids in the important fact that they do not form the starting point for a crown of "arms." Placed towards the summit of the calyx, at the angles of junction of the radials, are five triangular, rhomboidal, or pentagonal interradial plates, which have commonly been spoken of as the "deltoids" (fig. 327, A and B, *i*). The cycle of the deltoids is interrupted by the ambulacra, and a considerable portion of their entire area may be hidden from view beneath the adjoining plates

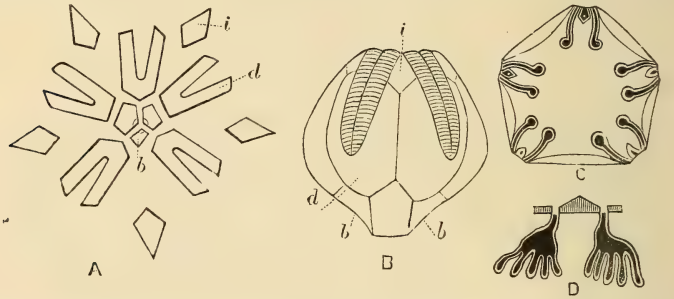

Fig. 327.—Structure of Blastoids. A, Calyx of *Pentremites*, dissected, showing the basals (*b*), the forked "radials" (*d*), and the interradial or "deltoid" plates (*i*). B, Side-view of the calyx of *Pentremites cervinus*—the letters as before. C, Section across the calyx of *Granatocrinus ellipticus*, showing the hydrospires cut transversely in their course below the ambulacral areas. D, Section across one of the ambulacral areas of *Pentremites Godoni*, showing the compound nature of the hydrospires, enlarged. (After Hall and Rofe.)

of the ambulacral fields. The "deltoids" of the Blastoids correspond very closely with the large interradials of *Cyathocrinus*, as shown in fig. 297, and, through these, with the interradial systems of the other Crinoids.

The most complicated structures in the test of the Blastoids are those connected with the ambulacral areas. The ambulacral fields (formerly spoken of as the "pseudambulacra") are always five in number, and pass in a radiating manner from the centre of the summit of the calyx to its margins. It is these which give to the summit of the body its resemblance to a flower-bud (figs. 327, B, and 328, A) upon which the name of the class is founded (Gr. *blastos*, a bud; and *eidos*, form). Though usually broad and petaloid in shape, the ambulacra are sometimes narrow, and their length varies in different types of the class. In a typical Blastoid, such as a species of *Pentremites*, the ambulacra have the following structure. Running down the centre of each of the petaloid ambulacral fields is a well-marked median groove, often with crenulated edges (fig. 329, B, *ag*), which in perfect specimens is roofed over by a double row of small calcareous ossicles or "covering-plates (fig. 329,

A, *c*). This median groove clearly corresponds with the "food-groove" of the arm and disc of a Crinoid, and may therefore be termed the "ambulacral groove." The ambulacral groove is excavated in the middle line of a long pointed plate (fig. 329, B, *l*) which runs down the centre of the ambulacral field and was termed by F. Roemer the "lancet-plate." The two halves of the lancet-plate, in well-preserved specimens, are seen to be crossed by numer-

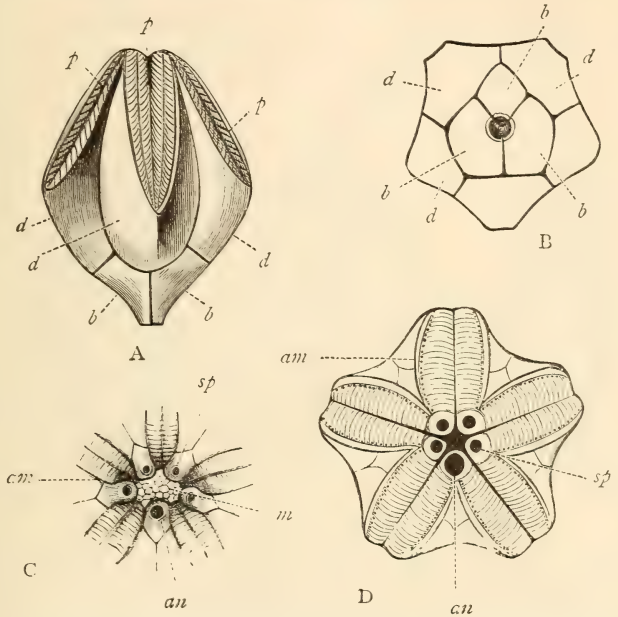

Fig. 328.—A, and B, Side-view and base of *Pentremites pyriformis*: *b b*, Basals; *d d*, Radials; *f f*, Ambulacral fields. C, Summit of *Granatocrinus Norwoodi* (after Meek and Worthen), enlarged, showing the plated membrane covering the mouth (*m*), the spiracles (*sp*), the anus (*an*), and the summits of the ambulacral fields (*am*). D, Summit of *Pentremites sulcatus* (after Ferd. Roemer), showing the mouth denuded of its covering-plates and placed in the centre of the spiracles (*sp*): *an*, Anal opening; *am*, One of the ambulacral fields. From the Carboniferous rocks.

ous transverse grooves, which open centrally into the main ambulacral groove. As the lancet-piece is narrower than the ambulacral field, there exists on each side of the former an interval, separating the sides of the lancet-plate from the forks of the bounding radial on each side. This interval is occupied on each side by a row of small quadrilateral ossicles or "side-plates" (fig. 329, *s*), which complete the ambulacral field superficially. Each ambulacral area is thus traversed from end to end by two lines of suture (fig. 329, B), which separate the median lancet-plate from the side-plates at its edges.

In *Pentremites* and in most other genera of Blastoids, the side-plates are so shaped as to leave along their outer ends a series of apertures or "marginal pores" (fig. 329, *p*), by means of which water is admitted to the "hydrospires." In many cases, however, the marginal pores are not merely spaces between the attenuated outer ends of the side-plates, but they are in part formed by a series of still smaller ossicles, which are known as the "outer side-plates" (the "supplemental pore-plates" of Roemer). In *Pentremites* the side-plates are marginal, and leave the whole upper surface of the lancet-plate exposed to view; but in other cases they encroach upon

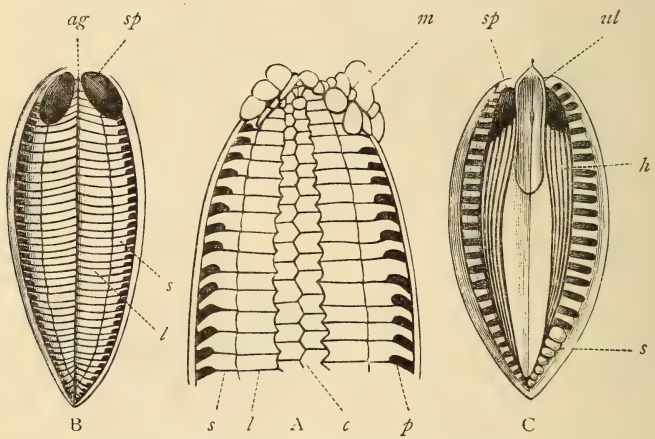

Fig. 329.—A, Upper portion of one of the ambulacra of *Pentremites sulcatus*, enlarged, showing the "covering-plates" (*c*) of the ambulacral groove, passing superiorly into the plated canopy (*m*) which conceals the mouth. B, Ambulacrum of *Pentremites pyriformis*, from which the covering-plates have been removed, showing the ambulacral groove (*ag*), the lancet-plate (*l*), the side-plates (*s*) with their marginal pores, and the spiracles (*sp*) at the upper end. C, Ambulacrum of the same species, from which the lancet-plate and most of the side-plates have been removed, showing the "under lancet-plate" (*ul*), the tops of the hydrospires, (*h*), and the ambulacral opening. (After R. Etheridge, jun., and P. H. Carpenter.)

the lancet-plate, and leave visible little more than the central food-groove.

The lancet-plate is pierced by a canal which lodged the radial water-vessel, and which opens into a circular ambulacral canal surrounding the mouth. The removal of the lancet-plate allows the top of the "hydrospires" to be seen (fig. 329, C, *h*). In the genus *Pentremites*, however, and in some other types, there is situated beneath the lancet-plate, in the middle line of the ambulacral field, an elongated, trough-like plate, which Messrs Etheridge and Carpenter have termed the "under lancet-plate" (fig. 329, *ul*).

True "arms," comparable with the structures so called in the Crinoids, are not developed in the Blastoids. Along the outer edge

of each ambulacral field there was situated, however, a single or double row of slender jointed "pinnules." The sockets for these are placed between each pair of marginal pores, but the delicate pinnules themselves are rarely preserved.

In perfect specimens of the Blastoids, the apex of the ventral surface (fig. 328, c) appears to have been closed by a canopy of small calcareous plates, some of which represent the orals of Crinoids; but in the majority of examples these have been destroyed in the process of fossilisation. In the Blastoids, therefore, as in the Palæocrinoids generally, the mouth was really subtegminal, and was not visible externally in the natural condition. When the covering-plates, however, have been lost, the mouth is seen as a central aperture placed at the point of convergence of the ambulacral fields (fig. 328, d). The vault of plates concealing the mouth passes laterally without a break into the "covering-plates" of the ambulacral grooves. The anus is excentric, and pierces one of the interradials ("deltoid" plates).

The most remarkable organs in the Blastoids are the respiratory tubes or "hydrospires," which are probably always present in one form or another, though they have not been universally detected. In *Pentremites* (fig. 330) the hydrospires lie underneath the lateral portions of the ambulacral fields, one on each side of each ambulacrum, so that there are ten of these organs in all. When the lancet-plate is removed from an ambulacrum in this genus, the outer sides of the hydrospires are seen on each side (fig. 329, c, *h*), with the "under lancet-plate" in the centre. Each hydrospire consists of a flattened lamellar tube, with thin calcareous walls, more or less extensively folded, and terminating internally by closed and somewhat dilated ends, the reduplications of the tube being placed lengthways beneath the ambulacrum. Water is admitted into the hydrospires by slits on their outer faces in direct connection with the rows of "marginal pores" between the overlying "side-plates" of the ambulacrum (fig. 330, *p p*). At their upper ends the hydrospires are placed in further communication with the exterior by a ring of five or ten openings surrounding the peristome. These apertures (formerly called "ovarian openings") are usually spoken of as the "spiracles" (fig. 328, c), and they probably served for the escape of water from the hydrospires.

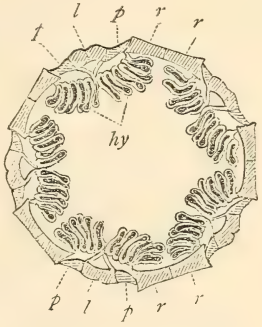

Fig. 330.—Cross-section of the calyx of *Pentremites sulcatus*, from the Carboniferous rocks of Illinois, somewhat enlarged, showing the transversely divided "hydrospires" (*hy*); *r r*, Radial plates; *l*, Lancet-plate; *p p*, Side-plates. (After Zittel.)

The general arrangement of the hydrospires in the majority of the Blastoids is essentially similar to that which obtains in *Pentremites*, as above briefly described; but there are some remarkable departures from this type. Thus in *Codaster* (=*Codonaster*) there are only eight hydrospires, and these open externally by slits separated by intervening ridges, which occupy four of the five interradial areas on the ventral surface of the body, and which have a direction parallel with that of the ambulacra (fig. 331, A). In *Phœnoschisma* the arrangement is the same, but the

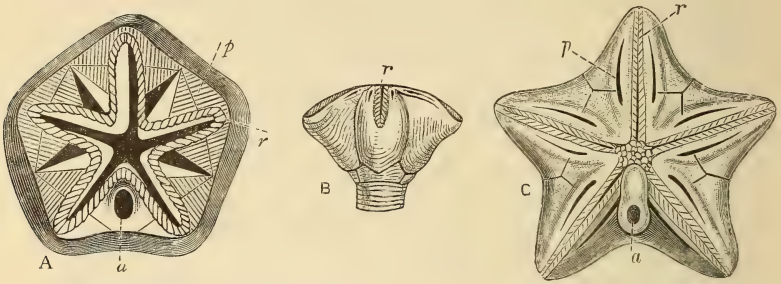

Fig. 331.—A, Upper surface of the calyx of *Codaster trilobatus*, var. *acutus*, from the Carboniferous Limestone, enlarged, showing the numerous hydrospire-slits (*p*) in all the interradii except the anal one. (After M'Coy.) B, Side-view of the calyx of *Orophocrinus* (*Codonites*) *stelliformis*, from the Carboniferous Limestone of North America, of the natural size. C, Upper surface of the calyx of the same (after Meek and Worthen), enlarged. *a*, Anal aperture; *r*, Ambulacra; *p*, in fig. C, Hydrospire-clefts or "spiracles."

hydrospire-slits occupy the anal as well as the other four interradii. Lastly, in the genus *Orophocrinus* (fig. 331, C) the "spiracles" or external openings of the hydrospires are in the form of ten clefts, of variable length, which extend along the sides of the ambulacra.

There can be little doubt that the "hydrospires" of the Blastoids, like the less highly developed structures of the same kind in the Cystoids, are essentially respiratory in function. They present in many respects a remarkable resemblance to the folded genital "bursæ" of the Ophiuroids, as regards both their structure and their mode of termination on the surface of the body. It is therefore probable that the hydrospires, like the "bursæ" of the Brittle-stars, were connected with the discharge of the reproductive elements into the external medium.

As regards the *distribution in time* of the Blastoids, no member of the order has been as yet certainly detected in the Ordovician rocks. In the Silurian rocks of North America a few forms have been found, and in the Devonian deposits both of the New and Old World various genera are represented, such as *Pentremitidea*, *Eleutherocrinus*, *Codaster*, and *Elæacrinus*. It is in the Carboniferous rocks, however, that the Blastoids attain their maximum development, the type-genus *Pentremites* (fig. 332, *a* and *b*)—sometimes written *Pentatremites* or *Pentatrematites*—appearing here for the

first time. The other genera most largely represented in the Carboniferous rocks are *Granatocrinus*, *Schizoblastus* (fig. 332, *c*), *Codaster* (fig. 331, A), *Orophocrinus* (fig. 331, B), and *Mesoblastus*. Above the horizon of the Carboniferous Limestone no remains of Blastoids have been as yet discovered.

As regards their *classification*, the Blastoids are divided by Mr Etheridge, jun., and Dr P. H. Carpenter, into the two primary groups or orders of the *Regulares* and *Irregulares*, the former including pedunculate types with a symmetrical base and having equal and similar ambulacra, while the latter comprises sessile forms

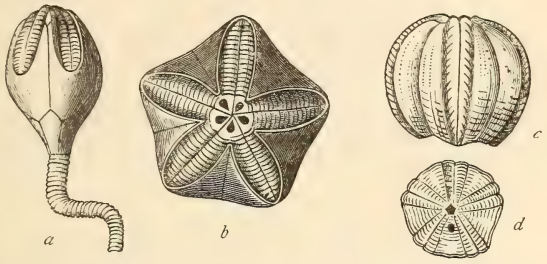

Fig. 332.—*a*, *Pentremites pyriformis*, viewed sideways, showing a portion of the column; *b*, Summit of the calyx of *Pentremites cervinus*, showing the ambulacral areas and the apical apertures; *c*, Side-view of *Schizoblastus melonoides*; *d*, Summit of *Schizoblastus neglectus*. (Figs. *a* and *b* are of the natural size; *c* and *d* are slightly enlarged.) (After Hall, and Meek and Worthen.)

in which the base is usually unsymmetrical, and one ambulacrum and the corresponding radial are different from their fellows. The following table exhibits the families adopted by the authorities just named, with the genera included in each :—

Order I. Regulares.

Family 1. *Pentremitidæ*.—Base usually convex and often much elongated. Spiracles five, but sometimes more or less completely divided by a median septum. Their distal boundary formed by side-plates. Hydrospires concentrated at the lowest part of the radial sinus. The genera *Pentremites* (fig. 328), *Pentremitidea*, and *Mesoblastus* are included in this family.

Family 2. *Troostoblastidæ*.—Ambulacra very narrow, and descending sharply outwards from the much-restricted peristome. Deltoids usually limited to the summit and rarely visible externally. Lancet-plate entirely covered by the side-plates. Spiracles generally double, appearing as linear slits at the sides of the deltoid ridge, but not bounded distally by side-plates. The genera *Troostocrinus*, *Metablastus*, and *Tricœlocrinus* belong here.

Family 3. *Nucleoblastidæ*.—Calyx usually globular or ovoidal, with flattened or concave base and linear ambulacra. Spiracles distinctly double, and chiefly formed by the apposition of notches in the lancet-

plate and deltoids. This family includes *Elæacrinus* (with an anal plate); and *Schizoblastus* (fig. 332, *c* and *d*), *Cryptoblastus*, and *Acentotremites* (without an anal plate).

Family 4. *Granatoblastidæ.*—Calyx globular or ovoidal, with a flattened or concave base and linear ambulacra. Spiracles five, piercing the deltoids; or ten, grooving their lateral edges. This family includes the genera *Granatocrinus* and *Heteroblastus.*

Family 5. *Codasteridæ.*—Base usually well developed and sometimes very long. Some or all of the hydrospire-slits pierce the calyx-plates on the sides of the radial sinus, restricted portions of which may remain open as the spiracles. This family includes the genera *Codaster* (fig. 331, A), *Phœnoschisma*, *Orophocrinus* (fig. 331, B and C), and *Cryptoschisma.*

Order II. Irregulares.

Family 6. *Astrocrinidæ.*—This family includes certain singular unstalked and unsymmetrical Blastoids, in which one ambulacrum and one radial are different from the rest. In *Astrocrinus* and *Eleutherocrinus* the basals are unsymmetrical, and the azygos radial is small and without definite limbs, its ambulacrum being short, wide, and horizontal. On the other hand, in *Pentephyllum* the basals are symmetrical, and the odd ambulacrum is linear.

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CHAPTER XXVII.

SUB-KINGDOM V.—ANNULOSA.

Characters and Divisions of Annulosa—The Scolecida and Anarthropoda.

Sub-kingdom Annulosa.—The Annulose animals are characterised by the possession of *a body which is usually more or less elongated, and is always bilaterally symmetrical instead of being radially disposed. Very commonly the body is divided into similar (homonomous) segments, which may be definite or indefinite, and are arranged along an antero-posterior axis. Lateral appendages may be absent or present, and when present, are symmetrically disposed. A nervous system is present, and consists of one or two ganglia placed in the anterior part of the body, or of a ventrally-placed, double gangliated chain.*

The sub-kingdom of the *Annulosa* may be divided into the three primary sections of the *Scolecida*, the *Anarthropoda*, and the *Arthropoda*, of which the two former are often separated to form a single great division of the animal kingdom under the name of *Vermes*. The division of the *Arthropoda* comprises the Crustaceans, the Arachnids, the Myriopods, and the Insects, the great majority of which are provided with a resisting exoskeleton, which is typically composed of chitine, but is often more or less largely calcified. Hence, the record of this division in past time is a comparatively complete one, its earliest representatives appearing in deposits of Cambrian age. The division of the *Anarthropoda* comprises the typical "Worms" (Leeches, Earthworms, Sea-worms, &c.), in which exoskeletal structures are often completely wanting, or are only partially developed. Hence the palæontological history of these animals is a necessarily very imperfect one. We have, however, unquestionable proofs of the existence of Sea-worms in rocks as ancient as the Ordovician, at any rate; and, if we may judge from the evidence of "tracks" or "burrows," the lower Cambrian

(and possibly even the Laurentian) deposits contain the remains of animals belonging to this division. Finally, the division of the *Scolecida* comprises the various "Worms" which from their commonly parasitic habit are generally known as the *Entozoa*, together with the group of the Wheel-animalcules or *Rotifera*. To say nothing of the microscopic dimensions of the Rotifers and many of the *Entozoa*, none of the Scolecids are provided with hard structures, which, under ordinary conditions, could possibly be preserved in the fossil state. It would, therefore, be no matter of surprise to find that we have absolutely no record of the existence of these animals in past time. There are, however, a few remains which have been referred to the *Entozoa*, and which may be noted here. The most satisfactory of these is a worm which was found by von Heyden in the abdomen of a fossil Beetle from the Miocene Brown Coal of Germany, and which has been referred to the Hairworms (*Gordiacea*) under the name of *Mermis antiqua*. The same genus has been detected in amber, along with minute filamentous worms which have been referred to the *Nematoda*, and have been placed under the genera *Anguillula* and *Enchytræus*. These are the sole remains of Scolecids which have hitherto been detected, and it is therefore unnecessary here to deal further with this division of the *Annulosa*.

Anarthropoda.

The animals included in this section are usually spoken of as "Worms," and constitute the highest division of the "*Vermes*," as this name is now understood. Under this head are placed the Spoon-worms (*Gephyrea*), the Arrow-worms (*Chætognatha*), and the Ringed Worms (*Annelida*), together with the small and aberrant group of the *Myzostomida*. The division is characterised generally by the usually elongated, vermiform body, which is, typically, composed of numerous, clearly recognisable segments. The segments are in general nearly similar: and when lateral locomotive appendages are developed, these are not composed of successive joints, and are not articulated to the body.

Of the four groups included under the head of *Anarthropoda*, the Annelides are comparatively well represented as fossils, commencing in the Cambrian period. On the other hand, the *Chætognatha* are wholly unknown in the fossil condition; as also are the Gephyreans, unless Ehlers be correct in referring to this group certain obscure remains from the Lithographic Slate (Jurassic) of Germany, for which he proposed the name of *Epitrachys*. The *Myzostomida*, however, have been certainly recognised in the fossil condition, though their geological history is still imperfectly known. *Myzostoma*, the type-genus of this curious and abnormal group,

comprises small, symmetrical, unsegmented animals, with a discoidal body furnished below with five pairs of unjointed feet terminated by hooks, which form cysts, somewhat like plant-galls, upon the calyx, arms, or pinnules of *Comatulæ* and other Crinoids. In various fossil Crinoids the arms or pinnules have been found to be distorted by the cysts of some form belonging to the *Myzostomida*, and further investigation will probably show that this group is really one of great antiquity.

Annelida.

The class of the *Annelida* comprises the so-called Ringed Worms, including the Leeches (*Hirudinea*), the Earthworms and their allies (*Oligochæta*), and the Sea-worms (*Polychæta*). The body in the Annelides is always elongated, and is composed of numerous segments, all the segments, except those at the anterior and posterior extremities of the body, being in general similar to one another. In the Leeches, the segments carry no lateral appendages, and locomotion is effected by means of suctorial discs. In the Oligochætous worms, the segments are provided with locomotive appendages in the form of horny setæ, embedded basally in the integument. Lastly, in the *Polychæta* the segments carry, as a rule, tufts of horny bristles attached to unjointed lateral protuberances or "foot-tubercles" (parapodia).

As regards their *distribution in time*, the *Oligochæta* are wholly unknown as fossils, and no reliable traces of the past existence of the *Hirudinea* have hitherto been discovered; though some problematical fossils from the Lithographic Slate (Jurassic) of Germany have been regarded as the remains of Leeches. The order of the *Polychæta*, on the other hand, comprises worms which are marine in habit and are at the present day very widely distributed, so that we should expect to find ample evidence of their former existence. As the integument of the Polychætous worms is more or less soft, and as the only hard structures developed within the tissues are the horny jaws and the locomotive bristles, it can only be under exceptionally favourable circumstances—as, for example, in the fine-grained Jurassic lithographic slates of Germany—that the actual *body* of these animals can have been preserved in the fossil condition. Many of the *Polychæta*, however, protect themselves by an investing tube which may be composed of lime, or of sand or other adventitious particles cemented together; and the cases of these "Tubicolous" worms are often preserved. The free-swimming or "Errant" *Polychæta*, again, have left evidence of their past existence in their fossilised jaws, as well as by less unequivocal remains in the form of filled-up burrows or meandering

trails upon the soft sand or mud of the sea-bottom. In this way we know that the Polychætous Annelides commenced their existence at least as early as the Cambrian, while obscure traces of their presence have even been detected in the Laurentian period. Owing to their comparatively frequent occurrence as fossils, it is necessary to study this group of Worms in greater detail.

Polychæta.

Sub-order I. Tubicola.—The Worms included in this sub-order are distinguished by the fact that they inhabit variously formed tubes, to which they are not organically connected, and in which they can move freely by means of their setigerous foot-tubercles. Owing to their possession of an investing tube, branchiæ are only developed in the anterior region of the body (fig. 333), this being the only part which is ordinarily exposed to the action of the sea-water; hence the *Tubicola* are sometimes called the "cephalobranchiate" Annelides.

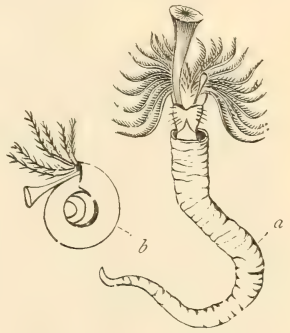

Fig. 333.—Tubicola. *a*, *Serpula contortuplicata*, showing the branchiæ and operculum; *b*, *Spirorbis communis*.

The protecting tube of the Tubicolous Annelides may be composed of carbonate of lime (*Serpula*), of grains of sand (*Sabellaria*), or of sand, pieces of shell, and other adventitious particles cemented together by a glutinous secretion from the body (*Terebella*); or it may be simply membranaceous or leathery (*Sabella*). Sometimes the tube is free and non-adherent (*Pectinaria*); more commonly it is attached to some submarine object by its apex or by one side (*Serpula* and *Spirorbis*). Sometimes the tube is single (*Spirorbis*, generally); sometimes the animal is social, and the tubes are clustered together in larger or smaller masses (*Sabellaria*).

When the tube is calcareous, it presents certain resemblances to the shells of some of the Molluscs, such as *Vermetus* and *Dentalium*. In the living state it is easy to make a distinction between these, for the Tubicolar Annelides are in no way organically attached to their tubes, whereas the Molluscs are always attached to their shell by proper muscles. In the fossil condition, however, it may be very difficult to refer a given calcareous tube to its proper place. As a general rule, however, the calcareous tubes of Annelides, such as *Serpula*, are less regular and symmetrical than those

of *Vermetus*, whilst the latter are partitioned by shelly septa, which do not exist in the former. Again, the tube of *Dentalium* is open at both ends, whereas it is closed at one extremity in the *Serpulæ*. In the Annelidous genus *Ditrupa*, however, the tube is open at both ends, so that this distinction is one not universally applicable.

Tubicolar Annelides are certainly known from the Ordovician rocks upwards, almost every great period having representatives of the order, though many of the fossils referred to this group are of a more or less problematical nature. The genus *Spirorbis* has survived from the Silurian period to the present day; and forms apparently not separable from the existing genus *Serpula* are known in deposits at any rate as old as the Carboniferous.

Of the fossil Tubicolar Annelides which are likewise known by still existing types, and the true relations of which are therefore beyond dispute, the three chief genera are *Serpula* (including *Vermilia* and *Filograna*), *Spirorbis*, and *Ditrupa*. In the genus *Serpula* (fig. 334), there is a long shelly tube, usually more or less tortuous, sometimes solitary, sometimes aggregated, which is fixed to some foreign body by a smaller or larger portion of its surface. The genera *Vermilia* and *Filograna* are principally distinguishable from *Serpula* proper by characters belonging to the animal and not to the tube which it inhabits. It is doubtful, therefore, if these three types can be separated in the fossil condition from one another; though it has been adduced as a distinctive character of *Vermilia* that the mouth of the tube often possesses from one to three tooth-like projections.

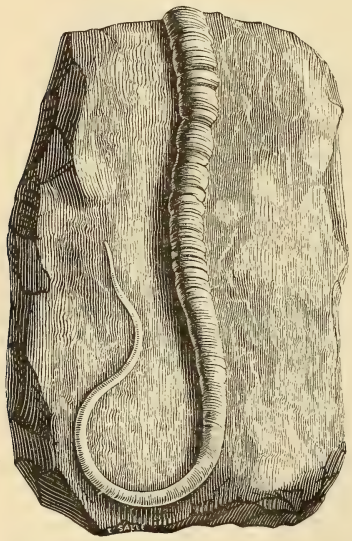

Fig. 334.—*Serpula flagellum*. Oxford Clay. (Jurassic.)

As regards its microscopic structure, the tube of *Serpula* appears to be mainly composed of delicate concentric laminæ of carbonate of lime, with a considerable proportion of animal matter. Some of the layers, and particularly those near the exterior, may be of considerable thickness, and may exhibit a peculiar tubulated structure, being traversed by minute branching canals, the direction of which is at right angles to the long axis of the tube itself (fig. 335, A). In other cases, the

tube is composed of numerous concentric laminæ separated by intervening rows of tolerably large-sized vesicles (fig. 335, B), while in other forms the laminated tissue preponderates and the vesicular tissue is imperfectly developed and is only present in parts of the tube.

As regards the geological range of *Serpula*, the earliest unequivocal types are found in the Carboniferous rocks,[1] but the genus has been asserted to occur in still older deposits. In the Trias and Lower Jurassic rocks *Serpulæ* are not infrequent, but are usually solitary in habit; whereas social types of the genus are not uncommon in the later Jurassic deposits, and entire beds of limestone in the Lower Cretaceous rocks are sometimes made up of the tubes of

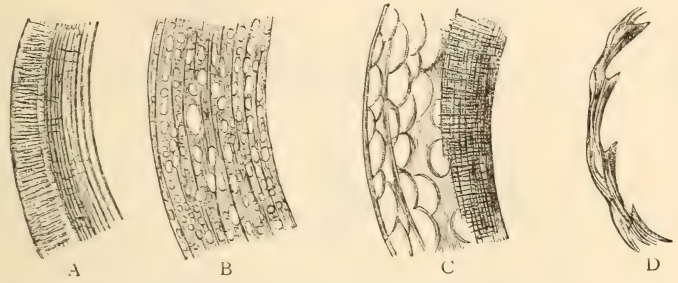

Fig. 335.—Microscopic structure of the tube of some Tubicolar Annelides. A, Cross-section of the tube of *Serpula* sp. (Recent), showing laminated and tubulated calcareous tissue; B, Cross-section of the tube of a Tertiary species of *Serpula*, showing laminated and vesicular tissue; C, Cross-section of the tube of *Cornulites* sp. (Silurian), showing an internal layer of laminated and tubulated tissue, with an outer layer of a vesicular structure; D, Oblique section of a tube of *Conchicolites gregarius* (Ordovician). The figures show only parts of the sections, and are all enlarged. (Original.)

these Annelides. Numerous forms likewise occur in the Tertiary rocks.

In the genus *Spirorbis* (figs. 336-338), the tube is calcareous, and is coiled into a flat spiral, one side of which is cemented to some foreign body. The spiral may be either right-handed ("dextral") or left-handed ("sinistral"), and the last volution is usually more or less elevated, and is often extended into a free bent tube of no great length. Internally the tube is usually open throughout, but in some forms it is divided into chambers by a few calcareous partitions. The tube is usually adorned externally with concentric striæ or annulations, sometimes with tubercles or spines; and all the known forms are of small size. In some species the tube is constantly solitary, but in other cases great numbers are found together. The

[1] The *Serpula parallela*, M'Coy, of the Carboniferous rocks, as previously shown, is really the siliceous "rope" of one of the Hexactinellid Sponges (*Hyalostelia*).

name *Microconchus* has been proposed for forms of *Spirorbis*, which are not simply cemented by the under surface to some foreign substance, but which make a depression or groove in the body to which the tube is attached. The living species of *Spirorbis* are all marine, but some of the extinct forms of the Carboniferous period are commonly found attached to the stems and leaves of undoubted terrestrial plants, a fact which would seem to show that some of these ancient types were able to exist in brackish, or, possibly, even in fresh water.

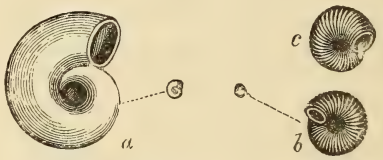

Fig. 336.—*a*, *Spirorbis omphalodes*, natural size and enlarged—Devonian, Europe and America; *b*, *Spirorbis Arkonensis*, of the natural size and enlarged; *c*, The same, with the tube twisted in the reverse direction—Devonian, America. (Original.)

Fig. 337.—*a*, *b*, *Spirorbis laxus*, enlarged—Silurian, America; *c*, *Spirorbis spinuliferus*, of the natural size and enlarged—Devonian, Canada. (After Hall and the Author.)

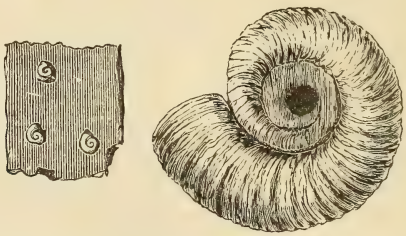

Fig. 338.—*Spirorbis* (*Microconchus*) *carbonarius*, natural size, attached to a fossil plant, and magnified—Carboniferous. (After Dawson.)

The earliest known species of *Spirorbis* occur in the Ordovician rocks, and the genus is abundantly represented in the Silurian, Devonian, and Carboniferous rocks, the tubes often occurring in great numbers attached to the exterior of shells or corals. The *Spirorbis helicteres* of the Carboniferous rocks sometimes occurs in the Carboniferous rocks of Scotland in quantities sufficient to make up bands of limestone of some thickness. Other species have been described from the Permian rocks, and the genus continues to be well represented in both Mesozoic and Tertiary deposits, while liv-

ing forms, apparently little different from the fossil ones, abound in recent seas.

In the genus *Ditrupa*, the tube is free and unattached, open at both ends, and calcareous in composition, its general aspect being very similar to that of the shell of a *Dentalium*. The genus appears to have existed in Carboniferous times, but it is not found in any abundance till the Tertiary period is reached. Species of this genus are abundant in the London Clay (Eocene) and in the Red Crag (Pliocene).

In the Palæozoic rocks there occur the remains of various organisms which have been commonly referred to the Tubicolous Annelides, but which differ more or less extensively in structure and character from any existing types, their precise nature being thus rendered more or less doubtful. Some of the more important of these may be briefly considered here. Among the most problematical of these are the fossils for which the names of *Serpulites* and *Trachyderma* have been proposed. Under the head of *Serpulites* are included smooth, arcuate, semi-calcareous, glossy, apparently unattached, tubular fossils, which sometimes reach a length of a foot, with a diameter of an inch. In the most typical forms of *Serpulites* the tube exhibits two small longitudinal ridges or tubular ribs, placed respectively along the convex and concave faces of the fossil; but these thickened borders do not appear to be constantly present. Forms of *Serpulites* are found in the Palæozoic rocks from the Ordovician to the Carboniferous inclusive, but their true affinities are by no means certain. The name of *Trachyderma* (apparently the same as the *Scolecoderma* of Salter) was proposed by Phillips for the casts of membranous, flexible tubes which are found in Ordovician and Silurian deposits. These are transversely wrinkled or plaited, and as they are usually found to cross the strata obliquely or vertically, it is probable that they are really Annelidous in their nature.

More remarkable than the preceding is the Ordovician, Silurian, and Devonian genus *Cornulites* (figs. 339, 340), in which the animal was solitary, and inhabited a conical calcareous tube of considerable size. The tube of *Cornulites* (fig. 339) is ringed with well-marked transverse annulations, and is usually ornamented with fine longitudinal striæ. The tube gradually tapers towards its lower end, where it appears to have been attached to foreign bodies, the attachment taking place by the pointed and usually bent initial portion of the tube, and not (as in *Ortonia*) by the whole of one side. Moreover, many adult examples show no signs of having been attached by the pointed base, so that the tube was probably not invariably fixed to foreign bodies, but may have been free. The tube may be three or four inches long, straight or slightly curved, and with a wide

aperture at its broad end. The internal cast of the tube has the form of a series of inverted conical rings, of small width, arranged in an imbricating manner. The most remarkable feature about *Cornulites* is, however, the peculiar micro-structure of the thick calcareous wall. Thin sections of the tube show that it is composed principally of lenticular calcareous vesicles of considerable size (figs. 335, C, and 339, B), resembling in form the vesicles of a Cystiphylloid coral. These vesicles are sometimes traversed by irregular laminated bands or fibrous layers, and a similar layer seems to line the interior, and cover the exterior of the tube. The inner laminated layer (fig. 335, C) is sometimes of considerable thickness, and is

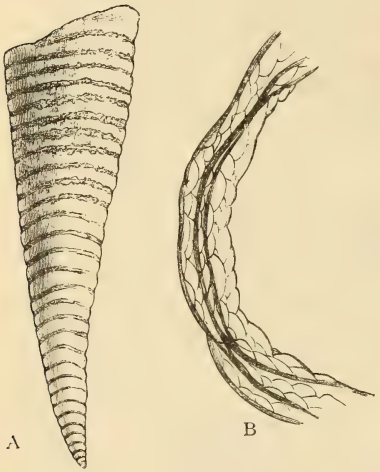

Fig. 339.—*Cornulites serpularius*, from the Wenlock Limestone. A, Tube of the natural size; B, Portion of a cross-section of the tube enlarged. (Original.)

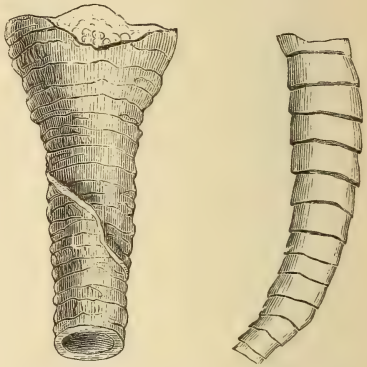

Fig. 340.—*Cornulites* sp. Silurian. The right-hand figure represents a cast of the tube. The left-hand figure represents a specimen broken below. (Original.)

traversed by minute transverse tubuli similar to those seen in the laminated calcareous tissue of some recent *Serpulæ*. As the tube in some *Serpulæ* (fig. 335, B) also shows a vesicular character, the microscopic structure of the tube of *Cornulites* is not so abnormal as it has generally been supposed to be, and its Annelidan nature is, on the whole, rather supported by its minute structure than disproved.

In the genus *Ortonia* (fig. 341) are included conical, slightly flexuous calcareous tubes, which have a general resemblance to *Cornulites*, but are of comparatively small size, and are cemented by the whole of one surface to some foreign body such as a shell or a coral. Though often found in considerable numbers, the tubes are essentially solitary in habit. The tube is ringed with imbricating

annulations, and the free surface of the tube, in some species, appears to have a cellular structure, similar to that which is seen in the tube of *Cornulites;* but the microscopic characters of *Ortonia* have not

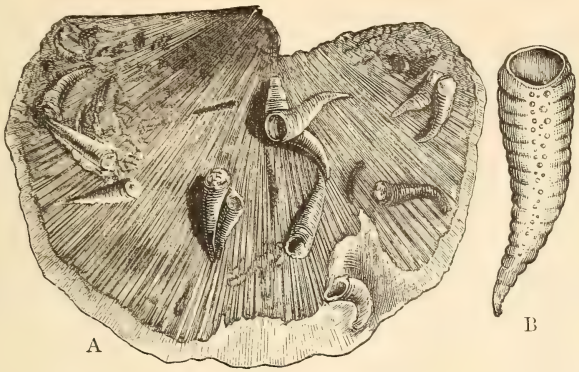

Fig. 341.—A, Tubes of *Ortonia conica* growing upon the valve of *Strophomena alternata*, natural size; B, A single tube of the same, enlarged. Ordovician. (Original.)

as yet been worked out. The known species of *Ortonia* are found in the Ordovician, Silurian, Devonian, and Carboniferous rocks. It may be noted in this connection that the tubes of some species of *Ortonia*, except for being attached along one side to foreign bodies, present a considerable general likeness to the tubes of the genus *Tentaculites*, which genus high authorities have regarded as Annelidan. There are, however, important distinctions between these two types, and the genus *Tentaculites* will be considered here under the *Pteropoda*, to which group, in the author's opinion, it is properly referable.

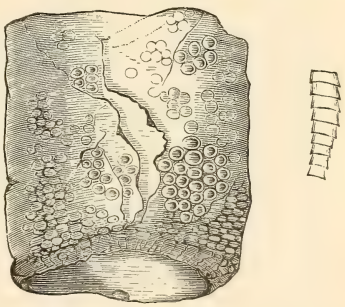

Fig. 342.—*Conchicolites gregarius*, growing upon the shell of an *Orthoceras*. Ordovician. (Original.)

A similar superficial likeness to *Tentaculites* is exhibited by the Ordovician genus *Conchicolites*, which is certainly Annelidan. In this genus (fig. 342) the animal was social, and formed masses of clustered tubes, growing side by side, attached by their bases to the outside of the dead shells of *Orthocerata* or Brachiopods. Each tube is made up of short imbricating rings, each of which partially overlaps the one below. Hence the cast of the tube (the right-hand figure in fig.

342) appears to consist of short conical segments, the broad ends of which are turned away from the mouth of the tube. Though the general aspect of the tubes of *Conchicolites* is very similar to that of *Cornulites*, the micro-structure of the tube is very different in the two genera. In *Cornulites*, as has been shown, the tube has a characteristic vesicular structure (fig. 335, c). On the other hand, thin sections of the tube of *Conchicolites* (fig. 335, D) show it to be devoid of this cellular structure, and to be composed of imbricating calcareous plates, which are fibrous in character, and which overlap in such a way that the broad upper ends of the successive rings are directed towards the interior of the tube.

SUB-ORDER II. ERRANTIA. — The Polychætous Annelides included in this sub-order are free-living animals which do not form for themselves investing-tubes. The body is usually elongated, each segment carrying on its sides tufts of horny setæ, attached to

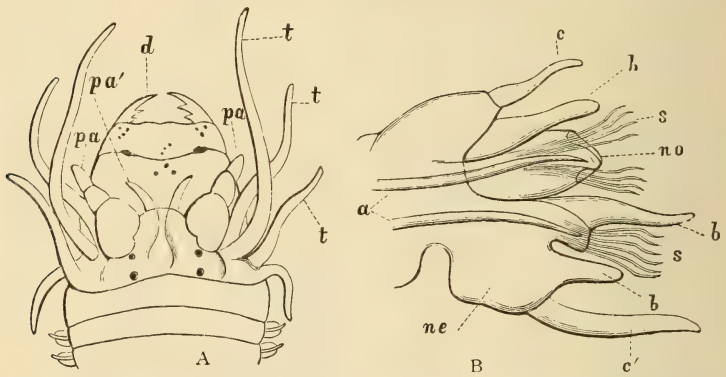

Fig. 343.—A, Head of *Nereis incerta*, viewed from beneath, and enlarged (after Quatrefages): *d*, The principal pair of chitinous jaws (the dark dots on the lobe behind these are smaller denticles); *pa'*, Internal pair of palpi; *pa*, External or greater pair of palpi; *t t t*, Tentacles. B, Foot-tubercle of *Nereis*, enlarged: *no*, Notopodium; *ne*, Neuropodium; *c*, Dorsal cirrhus; *c'*, Ventral cirrhus; *b b b*, Branchial filaments; *a*, Aciculæ; *s s*, Setæ attached to the dorsal and ventral oars.

fleshy, double tubercles or "parapodia" (fig. 343, B). The mouth is furnished with horny or partially calcified jaws (fig. 343, A). The branchiæ are attached to the sides of the body, or to the dorsal surface. Though the integument of the Errant Annelides secretes chitinous matter to a certain extent, a resistant exoskeleton is not developed, the only hard structures present being the chitinous setæ and the horny jaws, the lower pair of the latter (and sometimes the upper pair also) being more or less completely calcified. Owing to the soft nature of their integument and foot-tubercles, it can only be under the most favourable conditions that the actual *body* of an Errant Annelide can be preserved in the fossil state. Specimens

of this nature do, however, occur occasionally in finely-levigated sediments, such as the Lithographic Slates (Jurassic) of Germany and the Eocene Slates of Monte Bolca. Impressions of this kind not only exhibit the form of the body, but may show the lateral setæ (fig. 344) and the jaws in place; and upon such Ehlers founded the genera *Eunicites*, *Lumbriconereites*, and *Meringosoma*, all of which were originally described from the Lithographic Slates (Jurassic) of Germany.

Apart from the comparatively very rare cases in which, as above described, the body of the worm is itself partially preserved, it has been shown by Hinde and others that the horny jaws of Annelides are by no means of rare occurrence even in strata as ancient as the Ordovician, so that the Palæozoic seas must have been tenanted by vast numbers of these animals. The jaws of Annelides (fig. 345) usually present themselves as minute, dark, shining objects, wholly unconnected with one another, or with the remains of the animal to which they originally belonged. Though probably partly calcified, the jaws seem to be in the main composed of chitine, as they are not destroyed by the action of mineral acids. They average about $\frac{1}{12}$ inch in length, but a few reach a length of a third of an inch. In *form*, the jaws are very variable. In one type (fig. 345, A), the jaw is long and narrow, with a series of nearly similar teeth on one margin; in another common form, the jaw is furnished with a powerful anterior hook, which may be immediately succeeded by a series of small teeth, or may have the latter on the straight edge of a wide posterior extension (fig. 345, B); other varieties are in the shape of simple hooks with a wide flange-like extension behind (fig. 345, C); while others are falciform, with a series of small teeth on the curved upper edge. There are other variations in the shape

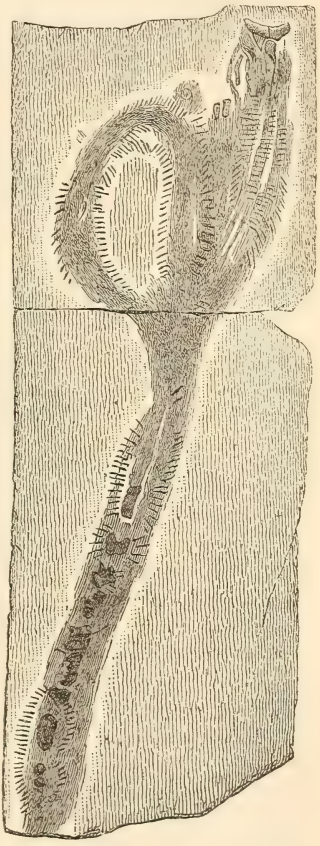

Fig. 344.—The impression of an Errant Annelide (*Eunicites avitus*), from the Lithographic Slates of Eichstadt, of the natural size. (After Zittel.)

of these minute fossils, and owing to the isolated condition in which they occur, it is difficult to refer them to genera and species. Most of the fossil forms resemble the jaws of the living family of the *Eunicea*, and such have been referred to the genera *Eunicites* (fig. 345, A), *Arabellites* (fig. 345, B), *Lumbriconereites*, &c. Others correspond with the recent genus *Glycera*, and have been placed under *Glycerites* (fig. 345, C); while *Nereidavus* appears to represent the existing family of the *Lycoridea*.

As regards their distribution in time, Hinde has shown that these fossil jaws are abundant in some parts of the Ordovician, Silurian, Devonian, and Carboniferous formations; and they are also known to exist in Mesozoic and Tertiary deposits in actual connection

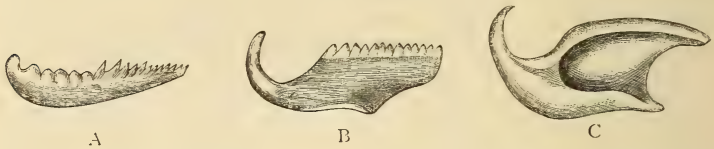

Fig. 345.—Jaws of Annelides from the Ordovician rocks (Cincinnati group) of North America. A, Jaw of *Eunicites varians*, enlarged 3½ times; B, Jaw of *Arabellites cornutus*, enlarged twelve times; C, Jaw of *Glycerites sulcatus*, enlarged fifteen times. (After Hinde.)

with the bodies of their original possessors. If Rohon and Zittel should prove to be correct in their view that the so-called "Conodonts" are really of the nature of the jaws of Annelides, then these minute fossils occur in rocks as ancient as the Upper Cambrian; but the nature of these problematical bodies will be dealt with more fully later on.

Apart from the above-mentioned indubitable remains of Errant Annelides, numerous more or less distinct worm-like markings, which are found in muddy and sandy sediments throughout almost the whole of the series of stratified rocks, have been referred to animals of this group. Some of these (such as *Nereites* and *Phyllodocites*) have been described as being of the nature of the petrified *bodies* of Sea-worms; but as they exhibit absolutely no *structure*, it is in the highest degree improbable that this explanation of their origin is correct. The true nature, in fact, of most of the remains here in question must be regarded as exceedingly uncertain. Some are, probably, really referable to the vegetable kingdom; others are almost certainly formed by Molluscs, or by Crustaceans; others are of entirely dubious affinities; while others are, doubtless, really due to the operation of Errant Annelides. It may be added that the fossil remains which have been referred to Nemertean Worms cannot at present be separated, in any satisfactory manner, from those formed by Errant Annelides. Thus the so-called *Nemertites*

of the Silurian is just as likely to be Annelidan as Nemertean, and the nature of the *Legnodesmus* of the Solenhofen Slates is wholly problematical. In fact, the entire subject of the remains of fossil Errant Annelides is one of the most obscure and difficult with which the palæontologist is called upon to deal; and all that can be done here is to glance at some of the leading points of interest connected with it, under the following heads :—

I. *Burrows of Habitation.*—Various recent Annelides live buried in the sand or mud, between tide-marks or in shallow water, and communicate with the surface by means of a perpendicular shaft or burrow. Such shafts may, for convenience' sake, be termed "burrows of habitation," though the animal forms a fresh one at will, as it moves from one spot to another; and, as a matter of course, they run in a direction more or less opposed to the surfaces of the laminæ of the rock, being often quite vertical. Sometimes

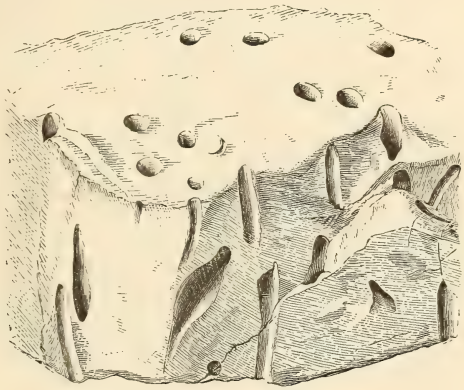

Fig. 346.—Annelide-burrows (*Scolithus Canadensis*) from the Potsdam Sandstone (Upper Cambrian). (After Billings.)

such burrows are hollow, but they are more commonly filled up by the matrix of the rock. Among the genera which have been founded upon remains of this kind are *Scolithus*, *Histioderma*, and *Arenicolites*, all of which occur in rocks of Cambrian or Ordovician age. *Scolithus* is founded upon long burrows, which are nearly straight, and descend vertically through the rock (fig. 346). They often become somewhat widened out superiorly, and are generally found in great numbers together. They occur abundantly in the Potsdam Sandstone (Upper Cambrian), and Clinton formation (Silurian) of North America, and also in the hard sandstones of the Stiper Stones in Shropshire (Ordovician). They have been supposed to have been formed by sea-weeds, but there is little doubt that they

are truly the burrows of Annelides. The somewhat problematical fossil upon which the genus *Histioderma* is founded is described as a curved burrow, from one to nearly four inches in length, terminating in a trumpet-shaped opening, which is placed in the centre of a small mound. The genus *Arenicolites*, again (fig. 347), includes small double burrows, which form loops, shaped like the letter U, opening on the surface by two apertures placed close to one another. The mouths of these burrows are thus placed in pairs, one orifice being supposed to be an aperture of entrance for the worm, and the other one of exit. Burrows of this nature occur abundantly in the Lower Cambrian strata of the Longmynd, and are also far from uncommon in deposits of Ordovician age.

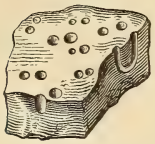

Fig. 347.—Burrows of *Arenicolites didymus*. From the Longmynd (Lower Cambrian).

II. *Wandering Burrows.*—Various recent Annelides, among which the common Lug-worm (*Arenicola piscatorum*) is a notable example, form long, wandering, irregular, and tortuous tunnels in the sand of the sea-shore, at a little distance below the surface. In these cases the worm subsists upon particles of organic matter disseminated through the sand or mud, through which, therefore, it literally eats its way. The burrows thus formed are, consequently, very irregular; they principally have a horizontal direction; if formed by many individuals, they may cross or intersect one another in various ways; and as the worm proceeds on its course, they become filled up in the rear of the advancing animal by the sand which has been passed through the alimentary canal, some of this sand being often voided at some point at the surface to form the tortuous "worm-casts," with which every wanderer on the sea-shore is so familiar. Bodies which we may reasonably assume to be of essentially the same nature as the filled-up "wandering burrows" of worms like the living Lug-worm, are well known to all workers amongst the more ancient, muddy and sandy strata of the earth's crust, and they have received various names, and have had very various origins ascribed to them. They usually present themselves as irregularly cylindrical, worm-like elevations of the surfaces of the strata (fig. 348), which usually are more or less parallel with the laminæ of deposition, but often run somewhat obliquely to these, so as to thread successive laminæ to one another. Generally, they differ slightly in texture and colour from the surrounding rock—as can well be supposed, if their origin be as above described—and from their somewhat superior hardness, they resist disintegration by weathering, and thus come to stand out prominently above the surface. Though they may be much matted together, and may thus appear to branch, it is only in some

cases that they really subdivide. It would appear that many of the fossils of the Palæozoic rocks which have been referred to the Fucoids, under the generic titles *Palæochorda*, *Palæophycus*, &c., may be really the filled-up burrows of wandering marine worms, and such remains may at present be grouped together under the common name of *Planolites*.

While the above explanation will account sufficiently for many of the objects which have been described under the name of *Palæochorda*, and which are here spoken of under the title of *Planolites*, there are many similar fossils for which Nathorst would account in a different and a quite satisfactory manner. It has been shown,

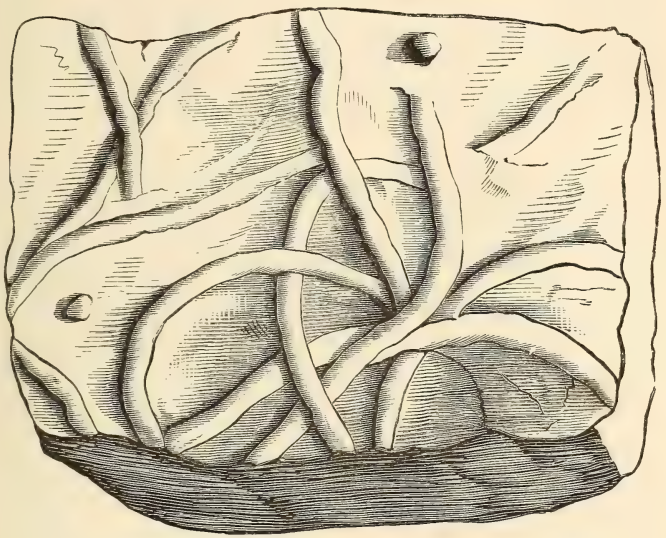

Fig. 348.—*Planolites vulgaris*, the filled-up burrows of a marine worm. Silurian (Clinton Group), Canada. (Original.)

namely, by this well-known observer, that plaster-of-Paris casts of the shallow grooves which worms make in crawling over the surface of fine mud, present cylindrical vermiform markings precisely similar in form and appearance to the fossils here spoken of under the name of *Planolites*. Nathorst therefore concludes that most, if not all, of such fossils are really *convex casts of what were originally grooves or furrows;* and he supports this contention by showing that the worm-like markings in question are found to stand out in demi-relief from the *under surfaces of the strata*. On this explanation—which would probably account satisfactorily for very many of these worm-like fossils—the structures here spoken of would really be of the nature of *tracks*, rather than of filled-up *burrows*. At the

same time, there are undoubtedly some examples which may be regarded as burrows and not as tracks, since there are specimens in which the cylindrical worm-like markings pass obliquely from one lamina to another, instead of being confined to a single surface of deposition. Another point that may be noted in connection with this subject is, that it has been shown by Nathorst that the tracks of certain Annelides upon the surface of mud or sand are *branched*. The fact, therefore, that many of the fossils described under such titles as *Palæochorda* and *Palæophycus* are seen to branch, would not be in itself sufficient to preclude acceptance of the explanation of their origin put forward by Nathorst.

In connection with the burrows of worms, a word may be said as to the curious vermiform bodies which occur abundantly in the Lithographic Slates (Jurassic) of Solenhofen, and which have been described under the name of *Lumbricaria*. The fossils in question are about as thick as a quill in some cases, but in others are only of the dimensions of twine, and they form convoluted and confused elevations on the surface of the beds. They have generally been looked upon as of the nature of casts of the alimentary canal—true "worm-casts" in fact—of marine worms; and, judging from their appearance, this explanation of their nature is probably correct.

III. *Trails and Tracks.*—Lastly, we have to deal briefly with a great group of fossils which have been supposed to be of the nature of the "trails" of Errant Annelides—that is to say, markings formed by the animal dragging its soft body over the surface of wet sand or mud, between tide-marks or in shallow water. Markings of this nature are extremely abundant in many of the older rocks, and in many cases no doubt can be entertained as to their being really the tracks of some marine animal. Even in these cases, however, it is at present impossible, in the majority of instances, to discriminate between the trails produced by Annelides and those formed by Univalve Molluscs or by Crustaceans. There are, nevertheless, certain tracks which may be regarded with considerable probability as Annelidan. This is especially true of the Silurian fossils upon which the genera *Nereites* (fig. 349, B) and *Phyllodocites* (fig. 349, A) have been founded. In these cases we have long, sinuous, and often sharply-bent impressions on the surfaces of the strata, which consist of a central, broader or narrower axis, representing the body of the worm, and of a series of lateral, more or less leaf-like markings, representing the foot-tubercles. These tracks, and others like them, have commonly been supposed to represent the actual *body* of the Annelide, now replaced by mud; but, as before remarked, it is very difficult to conceive of such a replacement, and it is more likely that we have simply the trail of the animal formed by its serpentine wandering over the surface of soft mud.

Another fossil, which is extremely abundant in the Silurian rocks of some localities, and which has generally been supposed to be the

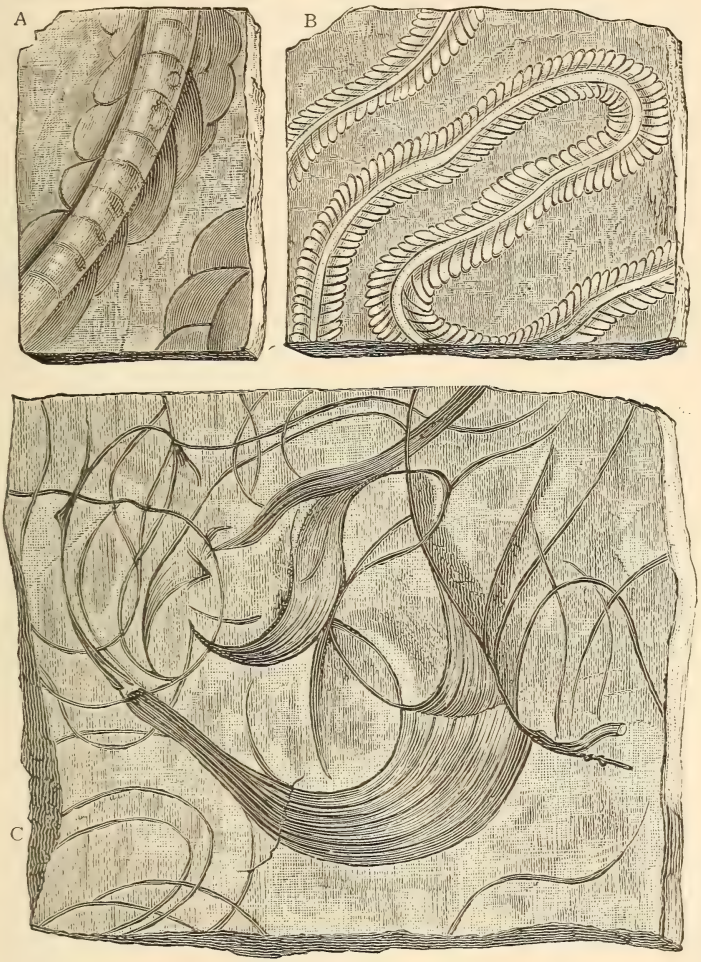

Fig. 349.—A, A small portion of the trail of *Phyllodocites Jacksoni*, from the Silurian slates of Wurtzbach, of the natural size (after Geinitz); B, Small portion of the trail of *Nereites Loomisii*, from the same locality, natural size (after Geinitz); C, Fragment of a slab, showing *Myrianites tenuis*, from the Silurian slates of Thornilee, Peeblesshire, of the natural size. The slab has split at different levels in different parts, and the fossil is seen to cut vertically across the laminæ of deposition, the surfaces thus formed being concentrically striated. (Original.)

track of an Annelide, is *Myrianites*. In ordinary specimens of this genus (fig. 349, C) all that is seen is that the surfaces of the strata are marked by winding and tortuous linear impressions, of extremely

small comparative width, and easily recognisable from the matrix by their darker colour and slightly different texture. These meandering markings wind over the surface of the stone in indefinite undulations, often appearing to cross one another; and no one, looking at such a specimen, would be inclined to doubt that he had to deal with the trails left upon the mud of the sea-shore by some soft-bodied marine animals, though he might question if these could be Annelides. Other specimens, however, of the same fossil, which have been carefully examined by the author, prove conclusively that, in spite of appearances, *Myrianites* is not only not Annelidan in its nature, but that it cannot possibly be the *track* of any animal whatever. It can be shown, in fact, that the narrow serpentine markings upon the surface of the stone, which are universally understood under the name *Myrianites*, are really *the cut edges of thin vertical laminar expansions, sinuously folded, and seen in horizontal section.* In fig. 349, c, a portion of one of the specimens referred to is

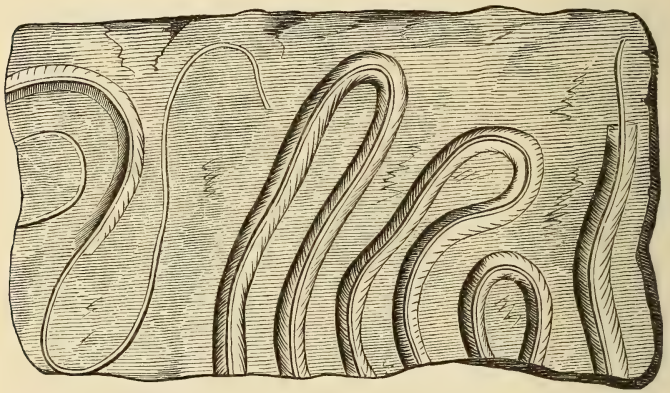

Fig. 350.—*Crossopodia Scotica*, a supposed Annelide track. Silurian. (After M'Coy.)

figured, from which it will be seen that the fossil *cuts directly across the laminæ of deposition*, its actual surface (where exposed by exfoliation of a part of the slab) being marked with concentric striæ. It is therefore quite clear that *Myrianites* was really a thin, erect, folded, leaf-like expansion, of some kind or another, and that what palæontologists have described under this name is only the horizontally-cut edge of this expansion as seen on the surface of the stratum. What *Myrianites* really is, is quite an open question. It is, perhaps, a peculiar form of Fucoid. That it is not Annelidan seems perfectly certain.

Another fossil which has generally been regarded as referable to the Errant Annelides is the *Crossopodia* of M'Coy (fig. 350), also

very abundant in certain Silurian strata. In this fossil there is a central narrow groove, which winds in serpentine bends over the surface of the stone, and is supposed to represent the body of the animal, bounded on each side by a broader and generally ill-defined space, supposed to represent the foot-tubercles. That *Crossopodia*, however, should be the petrified *body* of an Errant Annelide seems almost incredible, and that it is even the *track* of one of these creatures is extremely improbable. In well-preserved specimens of any size, the impressions known under this name are seen to wind backwards and forwards over the stone in a succession of long loops which are placed quite close together, and which could hardly have been produced by any animal in a movement of forward progression. There is, indeed, some evidence that the impressions of *Crossopodia* really cut directly across the laminæ of deposition to some depth, and that they have some direct, though at present not understood, connection with *Myrianites*.

As might have been expected, any fossils which can be supposed with any probability to be the tracks of Annelides, or of other marine animals, present themselves as *depressed* or *concave* markings on the upper surfaces of the strata. The *casts* of these markings, however, are often to be observed on the *under* surfaces of the beds, and these, as a matter of course, present themselves as *convex* or *elevated* impressions. When the beds are vertical, or when the specimens are not found actually *in situ*, it is impossible to distinguish between these two classes of specimens; especially as *some* elevated impressions, supposed to be tracks, do really occur on the *upper* surfaces of the strata. Such impressions, in the opinion of Principal Dawson, "have been left by denudation of the surrounding material, just as footprints on dry snow sometimes remain in relief after the surrounding loose snow has been drifted away by the wind, the portion consolidated by pressure being better able to resist the denuding agency."

As has been already pointed out, however, there is strong reason for accepting the conclusion of Nathorst that many of the elevated worm-like markings that are seen in muddy and sandy sediments are in reality *casts* of grooved tracks or furrows which have been produced by the movements of Annelides and other marine animals over fine silt.

Before leaving this obscure subject finally, it may be well to notice briefly one or two considerations which bear upon the question of the origin and real nature of markings such as we have been considering. In the first place, the late Mr Albany Hancock, in an extremely able memoir, advocated the view that the vermiform fossils of the older rocks may have been, in general at any rate, produced by *Crustaceans*. He showed that similar markings are

produced, at the present day, by small Amphipod Crustaceans (*Sulcator arenarius* and *Kröyera arenaria*), which burrow immediately below the sand on the sea-shore, and give rise to the following appearances: (1.) Large tracks, about 3-8ths of an inch wide, slightly raised, ribbon-like in shape, with a median groove, often intricate and convoluted, sometimes knotted, and several feet in length; (2.) Narrow wedge-shaped furrows, 2-10ths of an inch wide, winding capriciously and often abruptly over the surface; (3.) Nodulated or articulated tracks, consisting of a small furrow, with a rounded ridge on one side. Mr Hancock showed that tracks of these three kinds are actually produced by the above-named small Crustaceans, which burrow beneath the sand, but a short way below the surface, "the arch or tunnel thus formed partially subsiding, as the creature moves forwards, and breaking along the centre," thus giving rise to a median groove. There is no doubt that the phenomena so carefully observed by Mr Hancock throw considerable light upon the subject of the supposed Annelide tracks of muddy and sandy sediments; but there is room for much hesitation before concluding that any of these tracks, in the older rocks at any rate, were really formed by Crustaceans like the living *Sulcator arenarius*. One ground for such hesitation need alone be brought forward here—namely, that the so-called "Annelide-tracks" of the older Palæozoic rocks often occur in vast numbers, in finely-levigated deposits, and throughout a thickness of sometimes hundreds of feet of strata, and that it is almost inconceivable that traces of the makers should not have been detected in the same beds, supposing them to have been formed by animals which, like Crustaceans, have a skeleton highly susceptible of preservation in the fossil condition.

In the second place, there are good grounds for ascribing certain forms of "tracks," which have often been regarded as Annelidous, to the operation of Univalve Molluscs. It is well known that many Gasteropods, in crawling over the surface of sand or mud, give rise to sinuous or intercrossing trails, the general feature of which is the presence of a median furrow or groove, which may or may not be bordered by a series of lateral markings on each side. Thus, the annexed engraving (fig. 351) shows the track of a common living Gasteropod (*Purpura lapillus*) when moving over firm sand, and it will be at once seen that the markings produced by this Univalve are exceedingly similar to the supposed Annelide-trails upon which the genus *Crossopodia* has been founded, both consisting of a central groove, bounded by lateral raised margins. While it may therefore be regarded as very probable that some supposed worm-tracks have been formed by Molluscs, it cannot be altogether overlooked that we do not usually meet with the fossil shells of such Molluscs in

the deposits in which the trails occur, as we might reasonably expect to do.

Principal Dawson, again, suggests "that Algæ and also land-plants, drifting with tides and currents, often make the most remarkable and fantastic trails," which might easily be mistaken for the

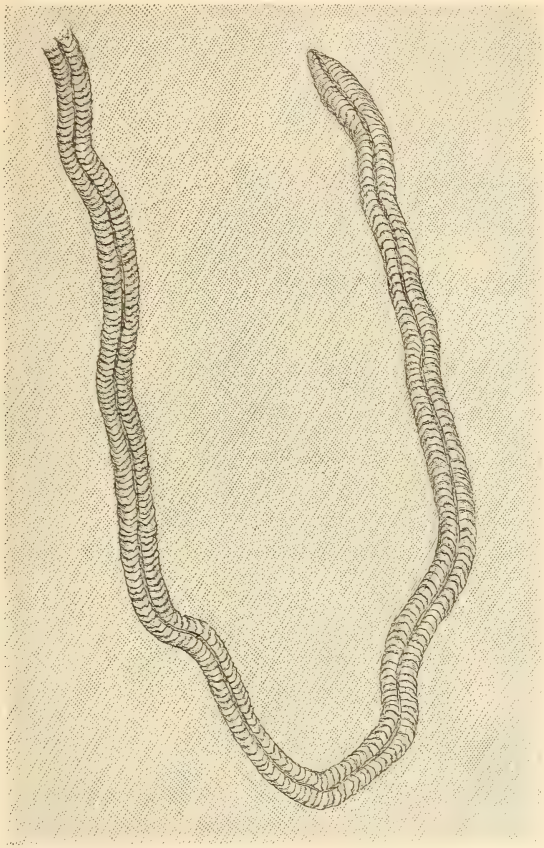

Fig. 351.—Track of the living *Purpura lapillus* on firm sand, reduced three diameters. (From a drawing made by the late Robert Gray.)

tracks of Annelides. This suggestion is a very valuable one, but certainly will not explain the origin of the majority of the so-called "Annelide-tracks" of the Palæozoic rocks, the regular serpentine form of which is one of their most remarkable features.

Lastly, some observers are disposed to see in these supposed tracks and trails the remains of various forms of *Algæ*, the drifted

stems of which, lying on the surface of mud or sand, have, by their slow decay, given rise to the worm-like markings which we have been here considering. The evidence in favour of this view does not appear to be satisfactory, but it is impossible to pursue further this intricate subject in this place. The student desirous of fuller information on this difficult question may be referred more particularly to the important and beautifully illustrated memoir which Professor Nathorst has published upon the tracks and markings produced by various living forms of Invertebrates.

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CHAPTER XXVIII.

ARTHROPODA.

Crustacea.

The division of the *Arthropoda* or "Articulate Animals" comprises the four great classes of the *Crustacea* (Lobsters, Crabs, &c.), the *Arachnida* (Spiders and Scorpions), the *Myriopoda* (Centipedes and Millepedes), and the *Insecta* (the Insects properly so called), and is distinguished as follows:—

The body is composed of a series of segments or "somites," which are usually definite in number, and which are arranged along a longitudinal axis. Each segment may be provided with a single pair of appendages, and these are always jointed, and are articulated to the body. Both the segmented body and the articulated appendages are, as a rule, furnished with a chitinous, often more or less extensively calcified, exoskeleton, formed by a hardening of the integument. The appendages are hollow, and the muscles are prolonged into their interior. The nervous system consists, typically, of a double chain of ganglia placed along the ventral surface of the body, united by longitudinal commissures, and traversed anteriorly by the œsophagus. The heart, when present, is situated dorsally. When distinct respiratory organs are present, they may be in the form of gills or branchiæ, or they may be saccular or tubular involutions of the integument (pulmonary sacs or tracheæ) adapted for breathing air directly.

If the King-crabs and the Eurypterids be retained in the *Crustacea*, then the classes of the *Arachnida*, *Myriopoda*, and *Insecta* comprise those Arthropods which breathe air directly, and which are thus, in general, adapted for a terrestrial life. On the other hand, the *Crustacea* are essentially water-breathing animals, and even those forms which are terrestrial in their habit, possess respiratory organs in the form of branchiæ. From their generally aquatic mode of life, and the usually more resistant character of their exoskeleton, the *Crustacea* are more abundantly represented in the

fossil condition than is any of the other classes. All the four great classes of Arthropods are, however, known to have been in existence in rocks as old as the Silurian, while the Crustaceans were thoroughly differentiated in the Cambrian period. It is, therefore, clear that the point of divergence of the four primary groups of Arthropods must be sought for in a period long anterior to the Cambrian; and it is hardly probable that we shall ever become acquainted with the primitive form from which the "phylum" of the *Arthropoda* took its origin.

Class I. Crustacea.

The class of the *Crustacea* may be generally defined as comprising *Arthropods which are essentially water-breathers, and usually are provided with gills or branchiæ. The segments of the body are usually definite in number, and some of them almost invariably carry jointed appendages. The head, typically, carries two pairs of antennæ; some of the appendages are modified to act as masticating organs; and the segments of the abdomen are commonly furnished with locomotive appendages. The body is protected by a chitinous or partially calcified exoskeleton or "crust," and the number of ambulatory limbs is mostly from five to seven. The Crustacea, in general, pass in development through a distinct metamorphosis, but the nature of this differs in different cases.*

The body of a typical Crustacean, such as a Lobster, generally exhibits a division into three regions—a *head*, a *thorax*, and an *abdomen* — each of which is composed of a certain number of somites, which may be free, or may be more or less indistinguishably fused with one another. Very commonly, the segments of the head and thorax are united together into a "cephalothorax," which may be protected by a common shield or "carapace" (fig. 352, *ca*). The segments of the abdomen may be separate and movable on one another, or a smaller or larger number of the terminal segments may be fused to form a caudal shield or "pygidium." The last segment of the abdomen (fig. 352, *t*) is known as the "telson," and is generally without appendages, while the anus opens on its lower surface. The "telson" has been variously regarded as an unpaired *appendage*, as a *segment* devoid of appendages, or as representing an aborted *region* of the body, the latter being the view which, on various grounds, seems to be the most probable one.

Each segment of the body of a Crustacean may be regarded as essentially composed of a convex upper plate ("tergum"), closed below by a flatter ventral plate ("sternum"), the line where the two unite being produced downwards and outwards, or

outwards only, into a plate which is known as the "pleuron" or "pleura" (fig. 353). Each segment of the body may carry a pair of appendages (even the telson being sometimes furnished with such); and the typical appendage of the *Crustacea* consists of an undivided basal portion, or "protopodite," to which are attached two diverging branches (fig. 353). The outer of these branches is termed the "exopodite," and the inner the "endopodite"; but one or other, or both, of these terminal divisions of the appendage may be suppressed.

The head in the *Crustacea* as a rule carries in front a pair of eyes, which in the higher forms are "compound," being made up of a variable number of separate lenses united side by side. The eyes may be fixed directly to the head, as in the "Sessile-eyed" Crustaceans (*Hedriophthalmata*), or may be carried upon longer or shorter movable peduncles, as in the "Stalk-eyed" Crustaceans (*Podophthalmata*). Behind the eyes, the head carries, in general, two pairs of jointed feelers or "antennæ," the first pair ("antennules") being comparatively small, while the hinder pair ("great antennæ") is of larger size. The segments immediately posterior to this carry three pairs of jaws—the "mandibles," and the first and second pairs of "maxillæ." All these are modified appendages, and therefore are in pairs, and work from side to side. The mandibles constitute the most powerful pair of jaws, and consist usually of a strong toothed protopodite to which a short endopodite (the "mandibular palp") is attached. Between the bases of the mandibles is the aperture of the mouth, bounded in front by an undivided chitinous plate (the "hypostome" or "labrum"), and behind by a usually forked lower lip or "metastoma." The first pairs of thoracic appendages are generally intermediate in structure between walking-legs and jaws, and constitute what are known as "foot-jaws" or "maxillipedes"; while the hinder ones are more especially devoted to locomotion. The thoracic appendages vary, however, extremely in form and

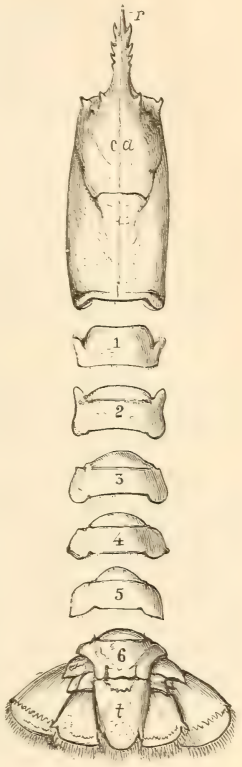

Fig. 352.—Lobster with all the appendages except the terminal swimmerets removed, and the abdominal somites separated from one another. *r*, "Rostrum"; *ca*, Carapace, covering the cephalic and thoracic segments. 1 to 6, The first six segments of the abdomen. No. 6 carries the last pair of swimmerets. *t*, Telson.

structure in different groups of the Crustaceans. In the Decapod Crustaceans five pairs of the thoracic appendages are in the form of walking-legs; while other groups (such as the Isopods) have seven pairs of ambulatory limbs; and in others, again, the number of locomotive thoracic limbs may be greater or less than the above. The abdominal appendages are very variable in form and function, but they are mostly primarily concerned in locomotion, though often modified to serve as respiratory organs, or, in the females, carrying the eggs.

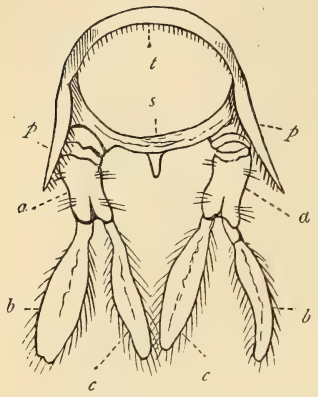

Fig. 353.—The third abdominal somite of the Lobster, separated. *t*, Tergum; *s*, Sternum; *p*, Pleura; *a*, Protopodite of the appendage; *b*, Exopodite; *c*, Endopodite.

As regards their classification, the *Crustacea* may be divided into the two primary sections of the *Entomostraca* and the *Malacostraca*. The first of these includes a great number of comparatively simple Crustaceans, in which the number of the segments and appendages is very variable, sometimes rising above the normal, and sometimes falling below it. The second division includes the more highly organised Crustaceans, in which the number of the segments and appendages is definite. The Cirripedes (with the *Rhizocephala*) may be provisionally regarded as a third division under the name of *Anchoracephala*, characterised by the fact that the adult is attached to foreign bodies by the metamorphosed head. The orders included in these three divisions are shown in the following table:—

Sub-class I. Anchoracephala.

Order 1. *Cirripedia.*

Sub-class II. Entomostraca.

Order 1.	*Ostracoda.*	*Legion*, Lophyropoda.
,, 2.	*Copepoda.*	
,, 3.	*Cladocera.*	*Legion*, Branchiopoda.
,, 4.	*Phyllopoda.*	
,, 5.	*Phyllocarida.*	
,, 6.	*Trilobita.*	
,, 7.	*Xiphosura.*	*Legion*, Merostomata.
,, 8.	*Eurypterida.*	

Sub-class III. Malacostraca.

Division A. Hedriophthalmata.

Order 1. *Amphipoda.*
„ 2. *Isopoda.*

Division B. Podophthalmata.

Order 1. *Cumacea.*
„ 2. *Stomatopoda.*
„ 3. *Schizopoda.*
„ 4. *Decapoda.*

As regards the general distribution of the *Crustacea* in time, remains of animals belonging to this class are abundant in the fossiliferous formations generally, from the Cambrian onwards. Nor are these remains confined to purely marine formations, since many Crustaceans are inhabitants of fresh or brackish waters, and the remains of such are of common occurrence in lacustrine or estuarine deposits. The most ancient group of the Crustaceans is that of the Trilobites, which is represented early in the Cambrian period, and continued to exist till the close of Palæozoic time (Permian). Nearly as old a group is that of the *Phyllocarida*, the latest representatives of which appear in the Trias. The Eurypterids, again, like the Trilobites, are exclusively Palæozoic, the earliest forms of this group appearing in the Ordovician period. Most of the other orders of Crustaceans appear to have come into existence within the limits of the Palæozoic period, though some doubt may be felt as to the systematic position and affinities of some of the ancient forms which have been referred to certain of the higher orders of the class. The Decapod Crustaceans, which represent the highest stage of development in the class, have their beginnings in the Palæozoic period, but they do not attain a dominant position till the Mesozoic deposits are far advanced, and they have attained their maximum at the present day.

Sub-class I. Anchoracephala.

Order Cirripedia.

The order of the *Cirripedia* includes a series of aberrant Crustaceans, of which the most familiar forms, and the only ones which occur in the fossil condition, are the Acorn-shells and their allies (*Balanidæ* and *Verrucidæ*) and the Barnacles (*Lepadidæ*). The essential feature of the order is that *the larva has the form of a free-swimming "nauplius," but the adult is fixed by means of its modified antennæ, and is enclosed in an integumentary sac, within*

which a many-valved shell is typically developed. The abdomen is rudimentary, and the thorax usually carries six pairs of multiarticulate limbs ("*cirri*"), *each of which consists of a protopodite carrying a long, jointed endopodite and exopodite.*

The typical *Cirripedia* are distinguished by the fact that in the adult condition they are permanently fixed to some solid object by the anterior extremity of the greatly metamorphosed head; the first three cephalic segments being much developed, and enclosing the rest of the body. The larva is free and locomotive, and the subsequent attachment, and conversion into the fixed adult, is effected by means of a peculiar secretion, or cement, which is discharged through the antennæ of the larva, and is produced by special cement-glands. In the *Cirripedia*, therefore, the head of the adult is per-

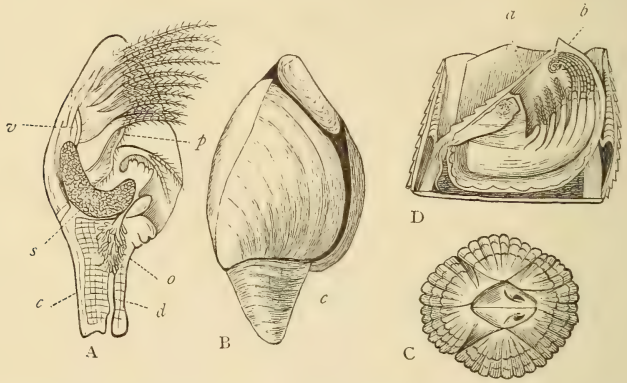

Fig. 354.—Morphology of Cirripedia. A, *Lepas pectinata*, one of the Barnacles, one side of the shell being removed, enlarged four times: *c*, Peduncle; *d*, Cement-duct; *o*, Ovary; *s*, Ovisac; *v*, Vas deferens; *p*, Penis. B, *Pœcilasma fissa*, enlarged five times; *c*, Peduncle. C, *Balanus balanoides*, viewed from above, of the natural size. D, *Balanus tintinnabulum*, with the shell on one side removed to show the animal; *a*, One of the valves ("scutum") of the operculum; *b*, Another valve ("tergum") of the operculum. (After Darwin and Pagenstecher.)

manently fixed to some solid object, and the visceral cavity is protected by an articulated calcareous shell, or by a coriaceous envelope (fig. 354). The posterior extremity of the animal is free, and can be protruded at will through the orifice of the shell. This extremity consists of the rudimentary abdomen, and of six pairs of forked, cirrated limbs, fringed with hairs, which are attached to the thorax, and serve to provide the animal with food. The two more important types of the *Cirripedia* are the Acorn-shells (*Balanidæ* and *Verrucidæ*) and the Barnacles (*Lepadidæ*). In the former the animal is sessile, the larval antennæ, through which the cement exudes, being embedded in the centre of the membranous or calcareous "basis" of the shell. In the latter the animal is stalked, and consists of a "peduncle" and a "capitulum." The peduncle consists of the

anterior extremity of the body, with the larval antennæ, usually cemented to some foreign body. The capitulum is supported upon the peduncle, and consists of a case composed of several calcareous plates, united by a membrane, enclosing the remainder of the animal.

The group of the *Rhizocephala* differs in many respects from that of the typical Cirripedes, cement-glands being absent, and the animal being fixed parasitically to the bodies of other Crustaceans by means of branched root-like processes derived from the metamorphosis of the antennæ, while the alimentary canal and limbs are absent.

The order of the *Cirripedia* is divisible into four principal divisions—the *Thoracica*, the *Abdominalia*, the *Apoda*, and the *Rhizocephala*—of which only the sub-order of the *Thoracica* is known to possess fossil representatives. This sub-order includes the Acorn-shells and Barnacles, in which the body is protected by a more or less complete calcareous shell; and as it is with the shell that the palæontologist has to deal, some details must be given as to its general structure.

As regards the microscopic structure of the shell, the calcareous tissue of the exoskeleton is exceedingly hard and compact, and shows in thin sections a finely granular structure. In the Lepadoids the shell-structure is very dense, with an obscure fibrous arrangement, but in many Balanoids a coarse cellular or tubular structure is present, the tubes being of large size, and being crossed by transverse partitions.

In the symmetrical Sessile Cirripedes or *Balanidæ*, commonly known as Acorn-shells, the animal is protected by a calcareous shell formed by calcifications within the walls of the first three cephalic segments. The animal is placed within the shell, head downwards, and is fixed to the centre of a shelly or membranous plate, which closes the lower aperture of the shell, and which is termed the "basis" (fig. 355, A, *l*). The "basis" is fixed by its outer surface to some foreign object, and is sometimes compact, sometimes porous. Above the basis rises a limpet-shaped, conical, or cylindrical shell, which is open at the top, but is capable of being completely closed by a pyramidal lid or "operculum." Leaving the operculum out of consideration at present, the sides of the shell are seen to be composed of from four to eight separate pieces or valves, or, as they are technically called, *compartments*. These compartments are usually closely contiguous by their lateral margins, and are separated by lines of division or "sutures"; but they are sometimes anchylosed together. Each compartment consists of a main central portion, which is termed the "paries" (fig. 355, B, *p*), and which is attached below to the "basis" of the shell. The "paries" grows downwards, so that the whole shell increases by additions made

round the base. The paries of each compartment is flanked by wing-like portions, which differ from the paries in appearance, and are called "radii" and "alæ," according to their shape (fig. 355, B, C). Sometimes the paries has a "radius" on both sides, sometimes "alæ" on both sides, and sometimes an ala on one side and a radius on the other.

The separate compartments of the shell receive special names according to their position. The compartment at the end of the shell where the animal thrusts out its cirrated limbs, is called the "carina" (fig. 355, A); and the compartment immediately opposite to this the "rostrum." The remaining compartments are "lateral," the one nearest the carina "carino-lateral," the one nearest the rostrum "rostro-lateral," and the middle one simply "lateral" (fig. 355, A); but the three rarely coexist.

The "operculum" or lid of the shell consists of two pairs of valves, known as the "scuta" and "terga," forming a little pyramid or cone, attached within the orifice of the shell by a membrane. Each scutum opens and shuts against its fellow along one margin (the "occludent" margin), and articulates with one of the terga

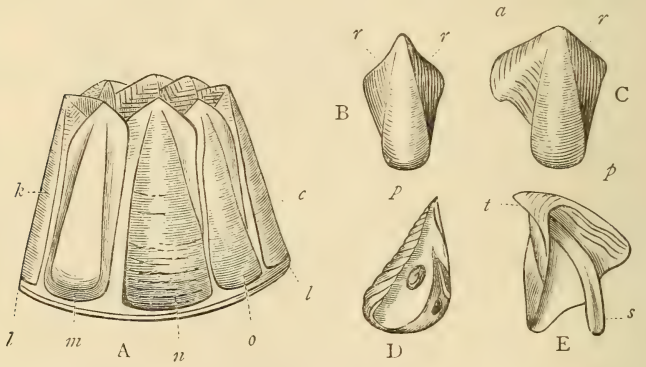

Fig. 355.—Shell of Balanidæ. A, Diagram of the shell of *Balanus*: *l l*, Basis; *c*, Carina; *k*, Rostrum; *m*, Rostro-lateral compartment; *n*, Lateral compartment; *o*, Carino-lateral compartment. B, Compartment with two radii (*r r*), flanking the paries (*p*). C, Compartment with a radius (*r*) on one side, and an *ala* (*a*) on the other side of the paries. D, Internal view of the scutum. E, Internal view of the tergum, showing the spur (*s*) and the beak (*t*). (After Darwin.)

along the opposite margin. Similarly, each tergum opens and shuts against its fellow along one margin (the "carinal" margin), and articulates with one of the scuta along the opposite margin. The apex of the terga (fig. 355, E) often forms a prominent beak, and the basal margin is furnished with a process or "spur." The scuta and terga are not only movable, but are furnished with proper depressor muscles.

As regards the *geological distribution* of the *Balanidæ*, the oldest known types are the *Protobalanus* and *Palæocreusia* of the Devonian rocks of North America. The former of these is a minute Balanoid which possessed the unique peculiarity that the shell consists of no less than twelve compartments (the "rostrum," the "carina," and five pairs of "lateralia"). In the genus *Palæocreusia*, again, the shell was embedded in the substance of the corallum of *Favosites*, and the compartments of the shell are fused to form a single undivided plate, covering a tubular sub-cylindrical basis.

With the above-mentioned exceptions, no Palæozoic representatives of the Balanoids have hitherto been recognised, the *Balanus carbonarius* of the Carboniferous rocks of Saxony being, according to Zittel, not a Cirripede at all. In the Mesozoic rocks, moreover, no undoubted representative of the Balanoids is known till the Upper Chalk is reached, a species of *Chthamalus* appearing in this formation. The fossil described by Seeley as a Balanoid from the

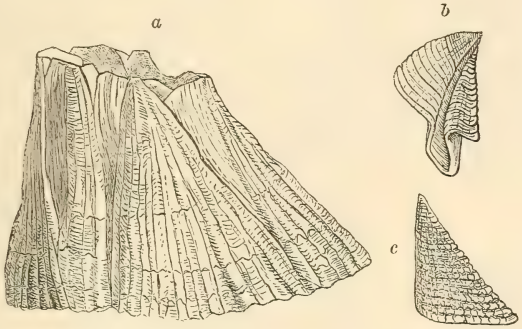

Fig. 356.—*Balanus concavus*, of the natural size, from the Pliocene Tertiary (Crag). *a*, Side-view of the shell; *b*, Tergum; *c*, Scutum. (After Darwin—copied from Zittel.)

Lias, under the name of *Zoocapsa*, does not appear to be properly referable to this group. In the Tertiary rocks, the remains of Balanoids are not uncommon, the recent genus *Balanus* (fig. 356) occurring in deposits as old as the Eocene, and being still more abundantly represented in the Oligocene, Miocene, and Pliocene. In the later Tertiaries the group is further represented by forms belonging to the genera *Chthamalus*, *Acasta*, *Pyrgoma*, and *Coronula*, all of which are known by living types.

The remaining family of the Sessile Cirripedes is that of the *Verrucidæ*, comprising only the single genus *Verruca*. In many respects the *Verrucidæ* approach the *Balanidæ*, but the shell is composed of six valves only, and is unsymmetrical, whilst the scuta and terga (forming the operculum), though movable, are not furnished with a depressor muscle. The *Verrucidæ* appear, so far as

is known, to have commenced their existence towards the close of the Secondary period, the Chalk having yielded two species. *Verruca Strömia* is found in the Coralline and Red Crags (Pliocene), in Glacial deposits, and in existing seas.

The third family of the *Cirripedia Thoracica* is that of the *Lepadidæ* or Pedunculated Cirripedes, commonly known as "Barnacles." In these (fig. 357) the animal differs from the Sessile Cirripedes in having its anterior extremity greatly elongated, forming a stalk or "peduncle" by which it is fixed to some foreign object. At its free extremity the peduncle bears the "capitulum," which corresponds to the shell of the Balanoids, and is composed of various calcareous pieces, united by a membrane, moved upon one another by appropriate muscles, and protecting in their interior the body of the animal with its various appendages. The peduncle is cylindrical, of varying length, flexible, and furnished with proper muscles. In some species the peduncle is naked, and cannot be preserved in the fossil condition; but in other cases the peduncle is furnished with calcareous scales (*Loricula* and *Turrilepas*, fig. 359), in which case it is readily preserved. The "capitulum" (fig. 358), as before said, corresponds with the shell of the *Balani*, and is generally much flattened. It consists ordinarily of five or more valves united to one another by membrane, usually with marked interspaces; but the valves may be rudimentary or wanting, and the entire capitulum may be membranous. The parts of the capitulum correspond ideally with the parts of the shell in the Balanoids. In the latter, however, the shell is for the most part composed of the "compartments," and the "operculum" is comparatively small and insignificant. In the Lepadoids, on the other hand, the valves which correspond with the operculum of the Balanoids are disproportionately developed, and the valves which correspond with the compartments of the Balanoids are much less conspicuous, and are often partially absent. The most important and persistent of the valves are the "scuta" (fig. 358, *b*), which protect the front part of the body, and correspond with the valves bearing the same name in

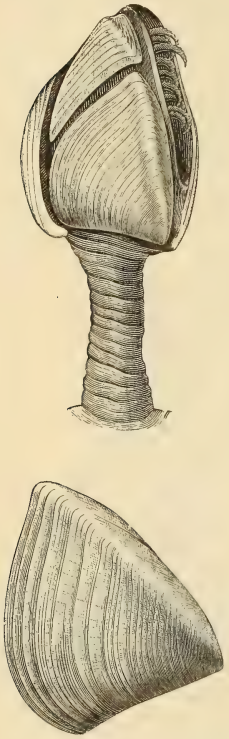

Fig. 357.—*Lepas anserifera*, a recent Pedunculated Cirripede. The lower figure shows the scutum detached.

the operculum of the Balanoids. The next most important are the "terga" (fig. 358, *a*), which protect the dorso-lateral surface. A pair of scuta and a pair of terga are present, and these are the largest of all the valves. The "carina" and "rostrum" are placed along the edges of the capitulum, the former being much the most important; and there may be a "sub-carina" and "sub-rostrum." The remaining valves, with the carina and rostrum, correspond with the proper shell of the Balanoids; but they are often wanting or rudimentary, and they require no further consideration here.

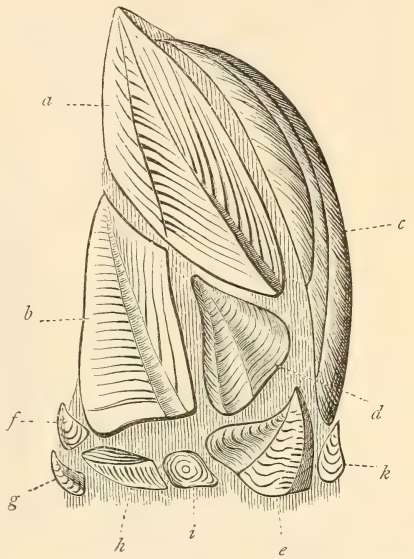

Fig. 358.—Capitulum of a Pedunculated Cirripede. *a*, Tergum; *b*, Scutum; *c*, Carina; *d*, Upper latus; *e*, Carino-latus; *f*, Rostrum; *g*, Sub-rostrum; *h*, Rostral latus; *i*, Infra-median latus; *k*, Sub-carina. (After Darwin.)

As regards the distribution of the Lepadoid Cirripedes in time, the oldest known types belong to the genus *Turrilepas* (=*Plumulites*), several forms of which have been detected in the Ordovician, Silurian, and Devonian formations. In this singular genus (fig. 359, *a*) are included elongated bodies covered with from four to six intersecting rows of calcareous plates. The plates are triangular in form, with a curved lower margin, and marked with transverse striæ; those of the median series being keeled. When detached and occurring in an isolated condition (fig. 359, *a*), these plates are not unlike the shells of certain Pteropods, while they may be, and have been, mistaken for the plates of Chitons. They are also not very unlike the plates of some Cystideans (*Ateleocystites*). By Barrande, *Turrilepas* was regarded as the capitulum of a Lepadoid, in which there was either no peduncle or a short one; but Dr Henry Woodward is probably correct in the view that the fossils really represent a scaly peduncle similar to that of the genus *Loricula*, and that the capitulum is still unknown. On the other hand, the *Strobilepis* of the Devonian rocks of North America seems to be really founded upon the capitulum of a Lepadoid. Allied to *Turrilepas* is the Silurian genus *Anatifopsis*, of which only the

detached valves are known, these being somewhat quadrilateral in shape, and having the lower part of the base marked out into one or two horizontal segments, which are more or less separated from the body of the valve. In the Carboniferous and Permian rocks no Lepadoids are known, but the genus *Pollicipes* is represented in the later Triassic (Rhætic deposits). Other forms of *Pollicipes* are Jurassic, but the genus attained its maximum of development in the Cretaceous period, at which time the group of the Lepadoids seems to have reached its culminating point. Tertiary species of *Pollicipes* are also known, and the genus survives at the present

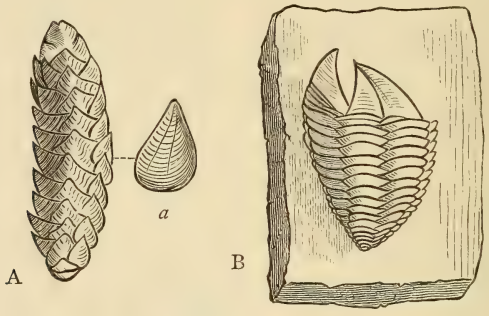

Fig. 359.—A, *Turrilepas* (*Plumulites*) *Wrightii*—Silurian. (After Woodward.) *a*, A plate of the same magnified. B, *Loricula pulchella*—Chalk. (After Darwin.)

day. Some Jurassic types formerly ascribed to *Pollicipes* have been separated by Zittel to form the genus *Archæolepas*. The genus *Loricula* is wholly Cretaceous, and comprises forms with a small capitulum and a short, plated peduncle (fig. 359, B), the organism being attached by one side to the shells of Ammonites. The extensive genus *Scalpellum* has numerous living types, and also about thirty fossil representatives, of which the oldest appears in the Cretaceous rocks. On the other hand, the recent genus *Lepas* (*Anatifa*) is not certainly known to occur in the fossil condition, even in the late Tertiary or Quaternary deposits, though the allied *Pœcilasma* is doubtfully represented in the newer Tertiaries.

CHAPTER XXIX.

CRUSTACEA—continued.

Sub-Class II.—Entomostraca.

Sub-class II. Entomostraca (*Gnathopoda*, Woodward). — The division of the Entomostracous Crustaceans includes a large number of comparatively simple types, in which the limbs and segments are usually indefinite in number, the former either fewer or more than fourteen; and the character of the appendages is very varied. The limbs are principally developed in the cephalic region, and their bases generally act as jaws. The characteristic larval form is that of a "nauplius." The orders of the *Eurypterida* and *Xiphosura* (with the probable addition of the *Trilobita*), here placed among the *Entomostraca*, are grouped together by Professor Claus in a special section, which he terms *Gigantostraca*, and which he regards as probably related to the *Arachnida*.

The *Entomostraca* are divided into three great divisions, or "legions," the *Lophyropoda*, *Branchiopoda*, and *Merostomata*.

Division A. Lophyropoda.

The members of this division possess few branchiæ, and these are attached to the appendages of the mouth. The feet are few in number, and mainly subserve locomotion; the carapace is in the form either of a shield protecting the cephalothorax, or of a bivalve shell enclosing the entire body. The mouth is mostly not suctorial, but is furnished with organs of mastication.

This division comprises the two orders *Ostracoda* and *Copepoda*.

Order I. Ostracoda.—*Small Crustaceans having the entire body enclosed in a shell or carapace, which is composed of two valves united along the back by a membrane. The valves are capable of being closed by an adductor muscle, the insertion of which in the interior of each*

valve is marked by a tubercle, pit, or group of spots, or by both spots and a pit. There are seven pairs of appendages, of which the first two are antennæ, and the posterior appendages are adapted for creeping or swimming.

The *Ostracoda* are all small Crustaceans in which the body is enclosed within a bean-shaped or mussel-shaped shell, composed of two valves united along the back by an elastic ligament (fig. 360, B). The animal can open the valves of the shell along their ventral margin, and can protrude the appendages and the caudal extremity of the abdomen. The first two pairs of appendages are antennules

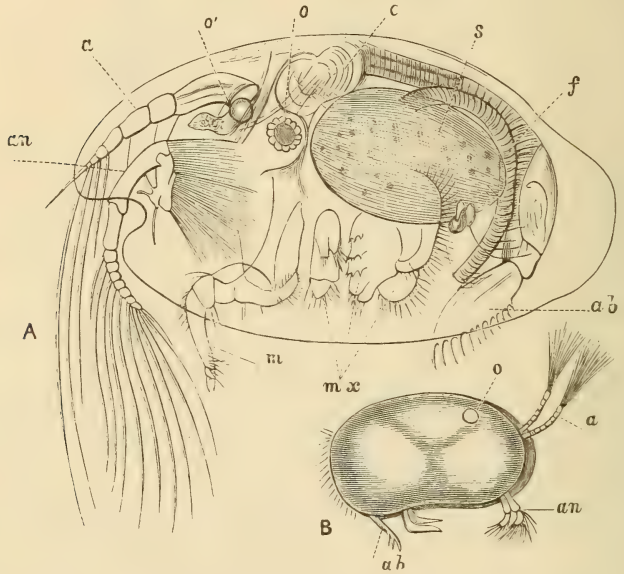

Fig. 360.—Recent Ostracoda. A, *Cypridina Messinensis*, viewed from the side, and greatly enlarged, one-half of the shell being removed. B, *Cypris fusca*, viewed from the side, and less highly magnified, the shell-valves being retained, but slightly displaced. *a*, Antennules; *an*, Antennæ; *o*, Eye; *o'*, Ocellus; *c*, Heart; *s*, Stomach; *f*, Whip-like appendage for the retention of the brood; *ab*, Extremity of the abdomen; *m*, Mandibular appendage; *mx*, The first, second, and third maxillæ.

and antennæ (fig. 360, A), which can be used as locomotive limbs. These are followed by a pair of mandibles, succeeded by a pair of maxillæ; and the next two pairs of appendages may be either jaws or legs. The sixth and seventh pairs of appendages are leg-like, and variously formed in different cases. A median eye, or two lateral eyes are present. Branchial plates are attached to some of the jaws, and a distinct heart may be present (*Cypridina*) or absent (*Cypris* and *Cythere*). The young forms are usually "nauplii," but

there may be no metamorphosis. Parthenogenesis is a not uncommon phenomenon in the Ostracodes.

The *Ostracoda*, often called "Water-fleas," are represented by very numerous forms both in fresh water and in the sea. The commonest fresh-water types are the little *Cyprides* (fig. 360, B). The marine Ostracodes (*Cythere*, *Cypridina*, &c.), are mostly shallow-water forms, and are of small size; but there are deep-sea types which attain comparatively gigantic dimensions (nearly an inch in length). Numerous fossil forms of the Ostracodes are known, their remains occurring in all formations, from the Cambrian onward.

It is only the carapace-valves of the Ostracode Crustaceans that are preserved in the fossil condition, with the rarest exceptions; and the general form of the carapace is often very similar in different genera. Hence the palæontologist has to rely, in the discrimination of these minute fossils, upon small variations of shape, differences in the thickness of the valves, the characters of the edges of the valves, or the manner in which they are hinged to one another, or, lastly, the surface-ornamentation. Besides the difficulty attaching to the study of the fossil *Ostracoda* from their small size and general similarity of appearance, it is often by no means easy to distinguish between the cephalic and the posterior extremity of the body. When not alike, the most contracted extremity is to be regarded as the head, and the widest as the hinder end of the carapace. The former, as a rule, carries grooves or tubercles, when such structures are present at all. The tubercles of the test, where developed, appear to represent the eye; and the grooves and intervening lobes, which are found in many forms, have been aptly compared by Barrande to the furrows and lobes of the glabella of Trilobites. There are many types, however, in which there are no conspicuous external markings, and in which the two ends of the carapace are similar. The Mesozoic and Tertiary *Ostracoda* are very small, and the same is true of a large number of Palæozoic species; but among the latter we find some comparatively large types, which, like *Leperditia Hisingeri*, may reach fifteen millimetres or more in length. As a rule, also, the Palæozoic *Ostracoda* are plain, or are simply striated or granular; whereas the Mesozoic and Tertiary forms are commonly ornamented with projecting tubercles, or in various other ways. As regards their general distribution in time, the *Ostracoda* certainly commence in the Upper Cambrian, and are even doubtfully represented in the lower division of this formation. They existed under many and varied types in the Ordovician and Silurian, and are abundant in all the succeeding formations, till the Recent period is reached. As matter of course, the remains of this group of Crustaceans with which we have chiefly to do, are principally those of the *marine* members of the order, and this is especially

true as regards the Palæozoic species. In later deposits, however, the occurrence of Ostracodes of types now found in fresh or brackish water is by no means uncommon.

The total number of fossil *Ostracoda* is very large, the difficulties attending their study, for reasons already stated, are quite exceptionally great; and it is impossible, in many cases, for the student to discriminate species, or, often, even genera, unless he should have made the group a subject of special investigation. Here, therefore, no attempt will be made to give even the briefest analysis of the families or genera of the order; but it may be well to shortly characterise some of the common or more remarkable types, with special reference to the Palæozoic forms, with which, upon many grounds, it is desirable that the student should have some acquaintance.

Among the Palæozoic Ostracodes, the first group that may be noticed is that of which *Leperditia* (fig. 361, C and D) is the type (*Leperditidæ*). In this genus the two valves are unequal in size, smooth, nearly oblong, bean-shaped, with the posterior end wider than the anterior. There is a small tubercular eye-spot, placed on the head, near the hinge, and underneath and behind this is a slightly inflated area, corresponding with an excavation of the shell interiorly, and exhibiting reticulated or areolar muscular markings. Behind the eye-spot is generally a vertical groove, which begins at the dorsal margin, and extends a short way across the valves. The genus ranges from the Ordovician to the Carboniferous. *Isochilina* (fig. 361, B) nearly resembles the preceding, but the valves are equal. It is not uncommon in the Ordovician rocks.

The genus *Primitia* (fig. 361, E–G) comprises another group of Palæozoic Ostracodes, which is essentially characteristic of the Cambrian, Ordovician, and Silurian deposits, though apparently also represented in the Carboniferous. In this genus the carapace is equivalve, convex, and oblong in shape, indented with a vertical dorsal groove of variable depth. Related to *Primitia* is the familiar genus *Beyrichia* (fig. 361, H and I), which is confined to the Cambrian, Ordovician, and Silurian rocks, and which sometimes is present in such vast numbers as to give rise, by the accumulation of the carapace-valves, to regular bands of limestone. The carapace of *Beyrichia* is more particularly distinguished by the possession of two or three transverse grooves, which start at the hinge, and pass partially or wholly across the valves. In the curious *Beyrichia* (?) *oculifera*, the eye-spot forms a prominent and faceted tubercle, unlike that of any other Ostracode (fig. 361, I). Two other members of the ancient family of the *Leperditidæ* may be just mentioned—namely, *Kirkbya* and *Moorea*, of which the former ranges from the Silurian to the Permian, while the latter is principally Carboniferous, and is doubtfully represented in the Jurassic rocks.

Another great group of the *Ostracoda* is that of the *Cypridinidæ*, in which the carapace is compact, smooth, or punctate, or striated, with a deep incision in the anterior margin for the exit of the larger

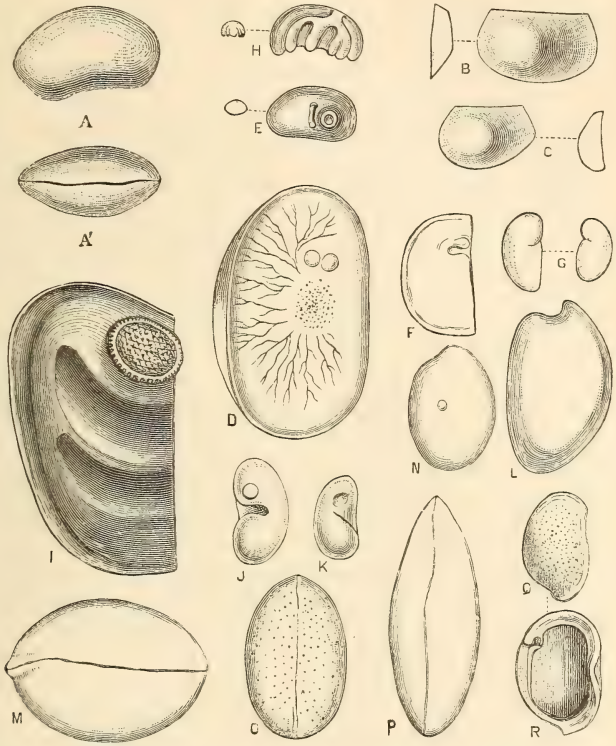

Fig. 361.—Types of Ostracoda. A, The test of *Cypris faba*, from the Miocene, viewed sideways, and enlarged fifteen times; A', The same, viewed from the dorsal margin; B, *Isochilina Ottawa*, enlarged four times (left valve and ventral view)—Ordovician; C, *Leperditia Josephana*, of the natural size (right valve and anterior view)—Ordovician; D, *Leperditia solitaria*, enlarged, showing the eye-spot and muscular impression—Silurian; E, *Primitia* sp.—Silurian; F, *Primitia strangulata*, Ordovician, enlarged; G, Right and left valves of *Primitia tarda*—Silurian; H, *Beyrichia complicata*—Ordovician; I, *Beyrichia* (?) *oculifera*, showing the elevated eye-spot, greatly enlarged—Ordovician; J, *Entomis tuberosa*, Jones (=*E. pelagica*, Barr.), right valve, enlarged twice—Silurian; K, *Entomis impendens*, enlarged—Silurian; L, *Cypridina Wrightiana*, left valve, enlarged four times—Carboniferous; M, Dorsal view of a small example of *Entomoconchus Scouleri*, enlarged four times—Carboniferous; N, Left valve of *Polycope simplex*, enlarged eight times—Carboniferous; O, *Cypris Brownіana*, viewed dorsally, enlarged twenty-five times—Pleistocene; P, *Candona candida*, viewed ventrally, and similarly enlarged—Post-Tertiary and Recent; Q, *Cythere convexa*, right valve, similarly enlarged—Pliocene and Recent; R, Interior of left valve of the same. (After Barrande, Rupert Jones, M'Coy, Hall, and G. S. Brady.)

antennæ. Numerous living forms of the *Cypridinidæ* are known, and the family is represented in past time principally by the three generic types, *Cypridina*, *Entomis*, and *Entomoconchus*, the last two

of these being entirely extinct. In *Cypridina* (fig. 361, L) the carapace is produced in front into a beak-like projection, below which is a hollow or notch facing the ventral margin. Many of the so-called *Cypridinæ* of the older Palæozoic rocks are now known to be referable to other types, but the genus is well represented in the Carboniferous, and exists at the present day. *Entomis* (fig. 361, J and K) ranges from the Ordovician to the Carboniferous, but attains its maximum in the Devonian rocks. The carapace in this genus resembles that of some of the *Leperditidæ* in having a dorsal groove, indenting the valves transversely, and sometimes reaching the ventral margin, and having a rounded tubercle placed at or near its lower end. One species of this genus (*Entomis serratostriata*), formerly known as a *Cypridina*, is so abundant in certain of the Devonian strata of Germany as to have gained for these the name of "Cypridinen-Schiefer." *Entomoconchus* (fig. 361, M), again, is a large form, with a thick and globose carapace, having a much less developed notch in front than in *Cypridina*. It is confined to the Carboniferous rocks. Among other Carboniferous *Cypridinidæ* may be mentioned the genera *Cyprella*, *Cypridella*, *Cypridellina*, *Sulcuna*, and *Rhombina*, all of which are characteristic of the Carboniferous rocks.

Another group of the Ostracodes (*Polycopidæ*) is that characterised by the genus *Polycope* (fig. 361, N), in which the carapace-valves are subequal and thin, not markedly notched in front, and having no beak. Though represented by living species, the only undoubted members of this genus which have been detected in a fossil state are from the Devonian and Carboniferous rocks.

The genus *Cytherella* is the type of another group (*Cytherellidæ*), in which the valves are very thick and calcareous, and are not notched in front. In *Cytherella* itself the right valve is much larger than the left, overlapping the latter throughout the whole circumference, and "presenting round the entire inner margin a distinct groove, into which the valve of the opposite side is received" (G. S. Brady). The genus ranges from the Carboniferous to the present day; and we may provisionally place with it the *Cytherellina* and *Æchmina* of the Silurian.

Lastly, we have the great group of Ostracodes represented by the families of the *Cypridæ* and *Cytheridæ*, "including all the fresh-water and a vast majority of the marine *Ostracoda*, and embracing all the forms classed by the earlier writers under the two great genera *Cypris* and *Cythere*" (G. S. Brady).

In the *Cypridæ*, as typified by *Cypris* itself (fig. 361, A and O), the valves are thin and smooth, and more or less sinuate below. Most of the *Cypridæ* are inhabitants of fresh water, and the fossil forms are principally found in lacustrine or fluviatile deposits, often

occurring in astonishing abundance. A few forms (such as *Bairdia* and *Pontocypris*) are marine in habit. The family of the *Cypridæ* seems to have attained its maximum at the present day, but is represented in deposits as old as the Carboniferous by forms which are believed to be referable to the living genera *Candona* and *Bairdia*. Specimens of the Carboniferous genus *Palæocypris* have been found, showing the eye, the antennæ, and the jointed limbs, of which there are two pairs behind the mandibles, the last pair being strongly incurved.

In the family of the *Cytheridæ*, lastly, the shell is minute, thick, inequivalve, and generally elongated or reniform in shape. The dorsal margin of the carapace has two denticles in the right valve fitting into corresponding sockets in the left valve. The surface is smooth, or is variously ornamented with tubercles or spines. The genera of *Cytheridæ* are mainly Recent and Tertiary; but the genus *Cythere* ranges from the Silurian to the present day, and there are various Secondary types belonging to the genera *Cythereis* and *Cytheridea*.

Order II. Copepoda.—*Small Crustaceans having bifid natatory feet, and the head and thorax usually covered with a carapace. Two caudal locomotive appendages are often present; but the abdomen does not carry limbs. Segmentation is distinct in the free forms; but it is more or less lost in the females of the parasitic types.*

The order of the *Copepoda* comprises numerous small Crustaceans, which inhabit both fresh and salt water, many types being parasitic in habit. No certain examples of the Copepods have hitherto been detected in the fossil condition.

Division B. Branchiopoda.

The Crustaceans included in this division have many branchiæ, and these are attached to the legs, which are often numerous, and are formed for swimming. In other cases the legs themselves are flattened out so as to form branchiæ. The body is either naked, or is protected by a carapace, which may enclose either the entire body, or the head and thorax only. The mouth is provided with organs of mastication.

The *Branchiopoda* comprise the *Cladocera*, the *Phyllopoda*, the *Phyllocarida*, and probably the *Trilobita*, though this last departs in many respects from the first three groups.

Order I. Cladocera.—The members of this order are *small Crustaceans, which have a distinct head, and have the whole of the remainder of the body enclosed within a bivalved carapace. The feet are few in number (usually four, five, or six pairs), and are mostly respiratory, carrying the branchiæ. Two pairs of antennæ are*

present, the larger pair being of large size, branched, and acting as natatory organs.

The types of this order are mostly confined to fresh water, a few forms being found in brackish pools. No undoubted representatives of the *Cladocera* have been hitherto detected in the fossil state, though a few small fossil types have been referred to this order.

Order II. Phyllopoda.—*Crustacea, mostly of small size, generally having the front part of the body protected by a shield-like carapace, or sometimes having the body enclosed in a bivalve shell. The feet are usually numerous, and more or fewer of them are leaf-like in form, and act as respiratory organs.*

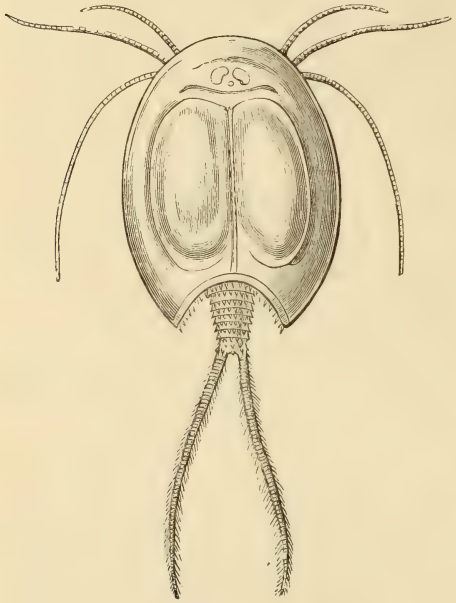

Fig. 362.—*Apus cancriformis*, a recent Phyllopod, viewed from above, and enlarged.

The living types of the Phyllopods (*Apus*, fig. 362, *Branchipus*, *Limnadia*, *Estheria*, &c.) are mostly inhabitants of fresh water, but species of *Estheria* are found in brackish water, and the *Artemiæ* live in salt lakes, or in the brine-pans of salt-works. As a type of the Phyllopods the recent genus *Apus* (fig. 362) may be taken, in which the anterior part of the body is covered with an oval carapace, carrying a pair of compound eyes upon its upper surface in front. The under surface carries sixty pairs of feet, of which the first is divided into three slender whip-like branches on each side, while the others are of the genuine "phyllopodous" type, being leaf-like in form, and acting as breathing-organs in function.

If the recent genus *Nebalia* and its numerous fossil allies are removed to form the order *Phyllocarida*, then the number of known fossil Phyllopods is comparatively small. By far the most important type, from a palæontological point of view, is the genus *Estheria* (fig. 363, a), which is nearly related to the living *Limnadia*, and

which in some respects constitutes a connecting-link between the Phyllopods and the Ostracodes. The body in *Estheria* is enclosed in a bivalve carapace, and the feet are foliaceous. The valves of the carapace have a well-marked beak or "umbo," and are hinged to one another along a dorsal line. From these circumstances, and from their being marked with numerous concentric lines of growth, the carapace-valves of *Estheria* very closely resemble the shells of certain Bivalve Molluscs (*Posidonia* and *Posidonomya*), for which they have often been mistaken. The valves are usually sub-triangular, ovate, or sub-quadrate in form, and they possess a horny texture.

The living *Estheriæ* are, without exception, inhabitants of fresh, or, rarely, brackish water; and no one of the recent twenty-four species has been detected in the sea. This would afford a strong

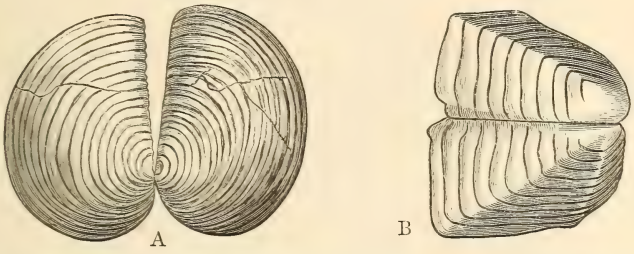

Fig. 363.—A, Carapace of *Estheria ovata*, magnified six diameters—Trias; B, Carapace of *Leaia Leidyi*, magnified five diameters—Lower Carboniferous. (After Rupert Jones.)

presumption that the deposits in which *Estheriæ* occur were laid down in fresh or brackish water; but such fossils not uncommonly occur in conjunction with undoubted marine remains. They appear, on the whole, to occur most frequently in those accumulations that "have been decidedly the result of brackish-water inundations, and of more permanent lagoons" (Jones). Fossil *Estheriæ* occur in the Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, and some Tertiary deposits; but they appear to have attained their maximum development towards the close of the Triassic period. The allied genus *Schizodiscus* is Devonian, and *Estheriella* is found in the Trias.

The genus *Leaia* (fig. 363, B) is very nearly allied to *Estheria*, and comprises small Bivalved Crustaceans, with "dark, horny, sub-quadrate valves, obliquely ridged from umbo to angles, and ornamented with distinct lines of growth parallel with the border" (Jones). *Leaia* is a very widely distributed genus, but all the known species belong to either the Carboniferous or Permian rocks. It has been suggested, however, that the obscure Ordovician genera *Myocaris* and *Ribeiria* are allied to *Leaia*.

Lastly, we may notice that a Phyllopod nearly allied to the living fresh-water genus *Branchipus* has been detected by Dr Henry Woodward in the Eocene formation, and has been described by him under the name *Branchipodites vectensis*. The much older *Branchipusites* (rightly *Branchipodites*) *anthracinus*, of the Coal-measures, has been supposed to have similar relationships, but it does not appear to be truly a Phyllopod.

Order III. Phyllocarida.—This order was founded by Packard to include the recent genus *Nebalia* along with certain extinct types of the *Crustacea*, which in some respects form a connecting-link between the Phyllopods and the Malacostracous group of the Schizopods, though they appear to be properly referable to the *Branchiopoda*. The principal living form of the *Phyllocarida* is *Nebalia*, which must be regarded as constituting with its immediate allies the family of the *Nebaliadæ*, and which must be taken as giving the essential characters of the order. In the genus *Nebalia* (fig. 364), the anterior part of the body is covered with a folded, but unhinged, cephalothoracic shield or carapace, which is connected with the body in its cephalic part only, and extends down the sides so as to enclose the mouth organs and the greater part of the other appendages. The valves of the carapace are not separated along the back, but are moved by an adductor muscle. In front of the carapace, and movably articulated to it, is a rostral plate; and there are also two compound stalked eyes, the cornea of which is not faceted. Two pairs of antennæ are present. The segments of the thorax, though enclosed by the carapace, are free, and carry eight pairs of foliaceous feet, which are of the "phyllopodous" type, and officiate as branchiæ. The abdomen is composed of free rings, the first four somites of this region carrying as many pairs of biramose legs, while there are also two pairs of rudimentary caudal limbs. No telson is present in *Nebalia* and its allies, but there is a well-developed telson in the *Ceratiocaridæ*. There is no metamorphosis in development.

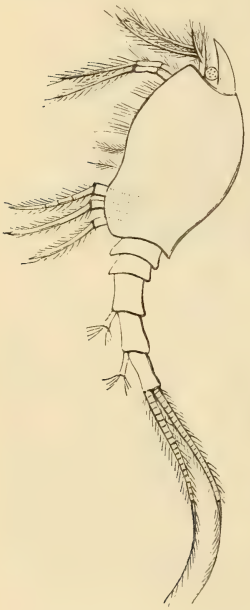

Fig. 364.—*Nebalia Herbstii*, enlarged about three times. Recent.

The living types of the *Phyllocarida* belong to the genus *Nebalia* and the closely related *Nebaliopsis* and *Paranebalia*, and are all small

Crustaceans, which are exclusively marine in habit. The recent forms constitute a special division of the order (*Nebaliadæ*), distinguished, among other characters, by the want of a telson; and they are not known to be directly represented in the fossil state. On the other hand, there are numerous fossil Crustaceans, chiefly of Palæozoic age, which appear to be properly referable to the *Phyllocarida*, and which may be regarded as constituting a special division of this order (*Ceratiocaridæ*), distinguished more particularly from the *Nebaliadæ* by the presence of a well-developed telson. The earliest forms of this peculiar group of "Pod-shrimps," as they have been termed, appear in the Cambrian period, while the group

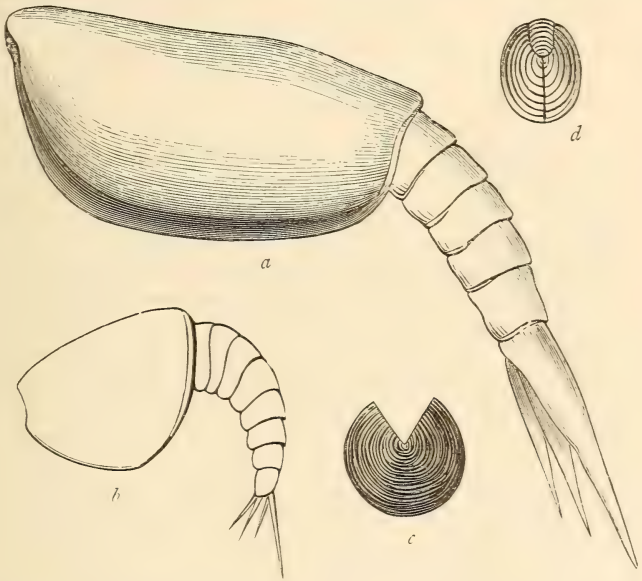

Fig. 365.—Palæozoic Phyllocarida. *a*, *Ceratiocaris papilio*—Silurian (Salter); *b*, *Hymenocaris vermicauda*—Upper Cambrian (Salter); *c*, *Discinocaris Browniana*, without the "rostrum"—Ordovician (Original); *d*, *Peltocaris aptychoides*—Ordovician (Woodward).

attains its maximum development in the Silurian, and underwent almost total extinction subsequent to the close of the Carboniferous period. The number of genera included in the family of the *Ceratiocaridæ* is very large, and many of these are only imperfectly understood. It will therefore be sufficient here to allude briefly to some of the more important and better known types.

As the type of this group may be taken the genus *Ceratiocaris* itself (fig. 365, *a*) in which the anterior portion of the body is enclosed in an elongated or pod-like carapace, composed of two oval

valves, contracted in front and with an abrupt posterior truncation. The carapace-valves are united along the back by a median line of attachment, and are commonly marked with fine linear striæ, while a lanceolate rostrum is developed in front. There were fourteen or more body-rings, of which the last five or six were free, some or all of these supporting lamellar appendages which seem to have been branchial in function. At the hinder end of the body is a powerful pointed telson, with two smaller lateral spines. The thoracic limbs are unknown, but toothed jaws have been in some instances recognised, either detached or in connection with the body of their former possessor. The oldest species of *Ceratiocaris* appear in the Ordovician rocks, but the genus attained its maximum in the Silurian period, and the last known forms occur in the Lower Carboniferous deposits. Some of the species attained to a great size, *C. Ludensis* growing to a length of two feet.

In the Cambrian rocks is found the allied genus *Hymenocaris* (fig. 365, *b*), in which the large sub-triangular carapace is not bivalved but is simply folded. There are generally nine free abdominal segments, the hinder termination of the body being adorned with three pairs of unequal spines. The Cambrian rocks of North America have yielded the remains of the related genus *Protocaris*, which differs from *Hymenocaris* principally in the possession of thirty narrow abdominal rings, and in the fact that there is a large telson ending in two terminal spines. Of the same general type as the preceding is the Ordovician genus *Caryocaris*, which agrees with *Ceratiocaris* in the fact that the carapace is bivalved, instead of being simply folded. The carapace is pod-like in form, and truncated behind, and the abdomen terminates in three spines. The researches of Novák have, further, shown that the singular Crustaceans described by Barrande from the Silurian rocks of Bohemia under the names of *Aristozoë*, *Callozoë* and *Orozoë*, and originally regarded by this observer as gigantic Ostracodes, are really referable to the *Ceratiocaridæ*. The carapace of *Aristozoë* (fig. 366) reaches three inches in length, and is composed of two valves united along a straight dorsal margin, its general shape being oval, with a pointed anterior and rounded posterior margin, and its front portion carrying prominent rounded tubercles. Novák has shown that the fossil described under the name of *Bactropus* is really a portion of the abdomen of *Aristozoë*, and that the so-called *Ceratiocaris debilis* is the telson of the same genus.

Of the later forms of the *Ceratiocaridæ*, the Devonian rocks of North America have yielded the remains of the curious genus *Echinocaris*, in which there is an ovoid folded carapace, adorned anteriorly with tubercles, and apparently without a rostrum. There are seven free abdominal segments, and a strong trifurcate telson.

Lastly, in the Carboniferous and Devonian genus *Dithyrocaris* (fig. 367), there is a broad carapace composed of two semi-oval valves ridged along the back in the middle line and laterally, and there is only one free body-ring. The rostrum is unknown, but there is a powerful trifurcate telson.

Another remarkable series of the *Phyllocarida* comprises forms with a thin, concentrically striated carapace, which may be simple, or may be divided into two halves and sutured along the back, and which is commonly notched in front for the reception of a triangular movable "rostrum." A number of curious, and in some cases problematical, fossils, the oldest of which are found in the Ordovician, while the last appear in the Trias, have been included in this group, and only a few of the more important can be noticed here. A typical genus of this group is the *Peltocaris* of the Ordovician rocks (fig. 365, *d*), in which the carapace is approximately circular,

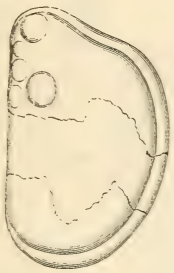

Fig. 366.—Carapace of *Aristozoë memoranda*, from the Silurian rocks of Bohemia, of the natural size, viewed sideways, with the dorsal margin to the left. (After Barrande.)

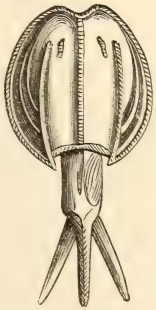

Fig. 367.—*Dithyrocaris Scouleri*, viewed from above, reduced slightly in size. Carboniferous Limestone. (After M'Coy.)

and consists of two valves of a semicircular form, which are united along the back by a straight dorsal suture, and which are deeply notched in front for the reception of a movable parabolic plate or "rostrum." The Ordovician and Silurian genus *Aptychopsis* is very similar in general characters to *Peltocaris*, but the rostrum is triangular in form. In the Silurian genus *Pterocaris* the same general type of structure is retained, but the valves are only united for a short space anteriorly, while they diverge behind, so as to form a wide posterior notch. On the other hand, in the remarkable Silurian genus *Discinocaris* (fig. 365, *c*), the concentrically striated carapace is circular in form, and shows no median line of suture on its dorsal surface, while there is a deep triangular notch in front for the reception of the rostrum. One species of this genus attains a diameter

of seven inches across the carapace. Various Devonian fossils have been placed, under special generic names, in the immediate neighbourhood of *Discinocaris*, and the Triassic genus *Aspidocaris* is also regarded as closely allied to this genus.

Order IV. Trilobita.—The Trilobites are Palæozoic Crustaceans in which *the body is more or less distinctly trilobed, and the head, thorax, and abdomen are distinct. The head is covered with a cephalic shield, which usually bears a pair of compound sessile eyes, ocelli being apparently never developed. The somites of the thorax are*

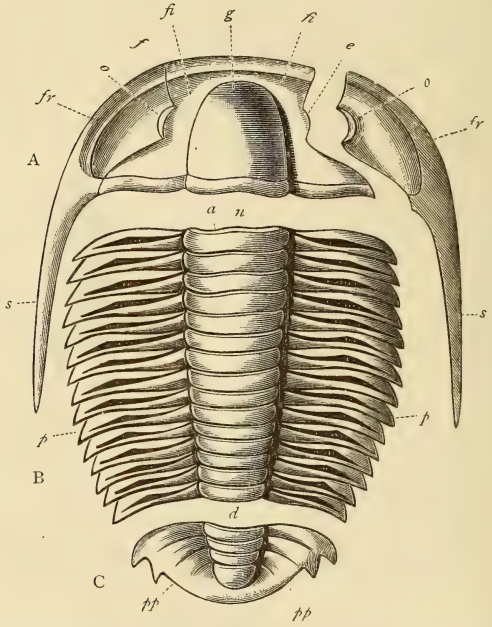

Fig. 368.—The skeleton of a Trilobite (*Angelina Sedgwickii*), partially dissected. A, Head-shield; B, Movable rings of the thorax; C, Tail or abdomen. *g*, Glabella, in this species without furrows; *fi*, Fixed cheeks; *e*, Eye-lobe; *o*, Eye; *f*, Facial suture; *fr*, Free cheeks; *s*, Head-spines; *p*, Pleuræ; *pp*, Anchylosed pleuræ of pygidium.

movable upon one another, and carry jointed legs to which branchiæ were attached. The abdominal segments are fused to form a caudal shield, and support below jointed appendages similar to those of the thorax. A well-developed upper lip ("*hypostome*") *is present, and some of the cephalic appendages are modified to act as mouth-organs.*

As regards the general structure of the *Trilobita*, the body was protected by a well-developed calcareous shell or "crust" which covered the whole dorsal surface of the body, and which usually

exhibits more or less markedly a division into three longitudinal lobes (fig. 368), from which the name of the order is derived. In some cases, however, as in the genera *Homalonotus* and *Illœnus*, this trilobation is only obscurely marked. Within the limits of the same species, Barrande has observed that the individuals may sometimes present themselves under two forms, one broad and the other long, and he regards the broad forms as the females, and the long forms as the males, of the species.

The crust exhibits a well-marked division into three regions, which are commonly found detached and separate from one another. These three regions are—1, a cephalic shield; 2, a variable number of movable "body-rings" or thoracic segments; and 3, a caudal shield or "pygidium."

The cephalic shield or buckler (fig. 368) is generally more or less semicircular in shape, and is composed of a central and two lateral pieces, of which the two latter may or may not be united in front of the former. The central portion of the cephalic shield is usually elevated above the remainder. It is termed the "glabella" (fig. 368, *g*), and it protected the region of the stomach. The form of the glabella varies a good deal. Usually it is widest in front (fig. 369), but its width may be nearly uniform, or it may be widest posteriorly and contracted in front, as in *Calymene*. The glabella is bounded at the sides by two grooves, which are known as the "axal furrows," and is marked off behind by a third groove, which is termed the "neck-furrow." The surface of the glabella may be quite smooth, but it is ordinarily divided into "lobes" by "grooves," which originate in the axal furrows, and pass inwards towards the middle line (fig. 369). These furrows mark the position of the segments which compose the glabella, and they are sometimes continuous from side to side. Usually there are three pairs of these furrows, a lower or basal, a middle or ocular, and an upper or frontal furrow; but there may be an additional pair of furrows in front of these. In some cases, as in *Illœnus* (fig. 374), the glabella is very indistinctly marked off from the rest of the shield.

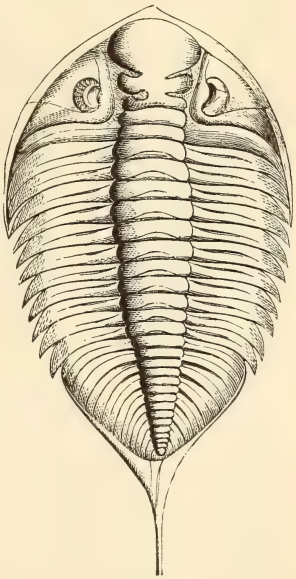

Fig. 369.—*Phacops* (*Dalmanites*) *caudata*. Upper Silurian.

The grooves of the glabella probably mark off so many *segments*, to which organs of prehension and mastication were attached inferiorly, and they are marked internally by corresponding ridges, to which muscles must have been attached. Sometimes (*Illænus*, *Ellipsocephalus*, *Encrinurus*, &c.) they are obsolete, as also occurs in particular species of other genera (*Trinucleus* and *Æglina*). Typically, three pairs of grooves are present, but some species of *Phacops* have four, and so have other types.

In certain Trilobites there are found two pores, or, in other cases, funnel-shaped depressions, one on each side of the glabella, in the axal furrow which separates this region from the cheeks. M'Coy thought that these "cephalic pores" might have been the points of origin of a pair of antennæ. It is certain, however, that this cannot be the true explanation of these structures; and they may be perhaps accounted for as marking the point of origin of deep internal processes of the exoskeleton to which muscles were attached, while it has also been suggested that they may indicate the position of a pair of "ocelli."

At each side of the glabella, and continuous with it, is a small semicircular area, which is termed the "fixed cheek" (fig. 368, *fi*). The glabella, with the "fixed cheeks," is separated from the lateral portions of the cephalic shield, termed the "movable" or "free" cheeks, by a peculiar suture or line of division, which is known as the "facial suture" (fig. 368, *f*). No such line of division is known to exist in any recent Crustacean; but there is a faint indication of it in *Limulus*, and some doubtful traces of it in certain other forms. The course taken by the facial sutures differs in different cases, and causes an important difference in the structure of the cephalic shield. In some cases (*Asaphus*, *Phacops*, *Homalonotus*, &c.) the facial sutures, starting from the posterior margins of the buckler, skirt the fixed cheeks, and join one another in front of the glabella. In these cases it is obvious that the free cheeks form a single piece, so that the entire shield consists of but two portions—1, the glabella and fixed cheeks; and 2, the amalgamated free cheeks. In other cases (*Paradoxides*, *Illænus*, *Proetus*, &c.), the facial sutures, instead of joining in front of the glabella, are continued forward, till they cut the anterior margin of the shield separately. In these cases the free cheeks are discontinuous, and the cephalic shield consists of three portions. In a few genera (as in *Trinucleus*, *Microdiscus*, and *Agnostus*) the facial sutures are absent, in which case the free and fixed cheeks are fused with one another.

The posterior angles ("genal angles") of the free cheeks are very commonly prolonged into longer or shorter spines, and the free cheeks also bear the eyes. The eyes are compound, and consist of an aggregation of facets, covered by a thin cornea. They are generally crescentic or reniform in shape, and are invariably *sessile*, in the sense that they are never supported upon movable stalks. In some cases, however, they are carried upon longer or shorter prominences. The eyes differ much in size, and they are wanting in a

few forms, such as *Agnostus*, *Ampyx*, some of the *Trinuclei*, and certain forms of *Conocephalus*. Though facets are usually easily detected in such as have eyes of any size, there are some (*Bronteus*, *Arethusina*, *Proetus*, &c.) in which the eyes are smooth. In any case, the number of lenses varies greatly, there being as few as fourteen facets, or as many as fifteen thousand in each eye in different types (Barrande).

Behind the cephalic shield comes the thorax, composed of a variable number of segments which are not soldered together, but are capable of more or less movement upon each other. The amount of movement thus allowed varies, but in several genera (*e.g.*, *Calymene* and *Illænus*) it was sufficiently great to allow of the animal completely rolling itself up after the manner of a hedgehog. The number of body-rings or segments in the thorax varies from no more than two (*Agnostus*) to as many as twenty-six (*Harpes ungula*), or twenty-nine. Ordinarily the thorax (fig. 373) is strongly trilobed, and each body-ring exhibits the same trilobation, being composed of

Fig. 370.—*Bronteus lunatus.*

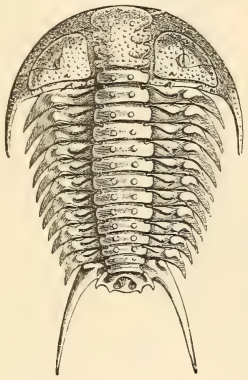

Fig. 371.—*Cheirurus pleurexanthemus.*

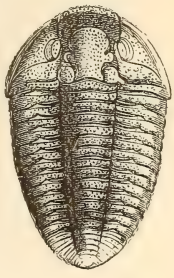

Fig. 372.—*Calymene Blumenbachii.*

a central, more or less convex portion, called the "axis," and of two flatter side-lobes, termed the "pleuræ." The pleuræ are in one piece with the axis, but are separated from it by a more or less pronounced groove, the "axal furrow." In one type of pleuræ, each of these structures carries a deep longitudinal groove or sulcus upon its upper surface (as in *Asaphus*, *Ogygia*, *Phacops*, *Calymene*, &c.) In another type, on the other hand (as in *Cheirurus*, *Bronteus*, *Acidaspis*, &c.), the place of the sulcus is taken by a similarly situated oblique *ridge*. The pleuræ are always bent downwards towards their ends, and also commonly bent backwards as well, the point where the backward curvature begins being the "fulcrum" of Salter. In the Trilobites

with grooved pleuræ, more especially, the pleuræ imbricate and overlap; and the "fulcrum" of each is often bevelled off, so as to form a facet upon which the pleura immediately in front plays, thus allowing the animal to *roll up*. In the state of complete enrolment, the under surface of the pygidium is closely applied to the corresponding surface of the head-shield, thus entirely concealing the ventral aspect of the animal. Some forms (such as *Homalonotus*, *Lichas*, *Triarthrus*, *Olenus*, *Paradoxides*, *Æglina*, &c.) are not known to have been endowed with the power of rolling up. Though the trilobation of the thorax is usually very well marked (figs. 370-373), at other times the axis is very broad, and the axal furrows more or less inconspicuous. This is the case in *Illænus* (fig. 374), and to a less extent in *Homalonotus*.

The caudal shield or "pygidium"—commonly called the "tail"—is composed of a greater or less number of segments anchylosed

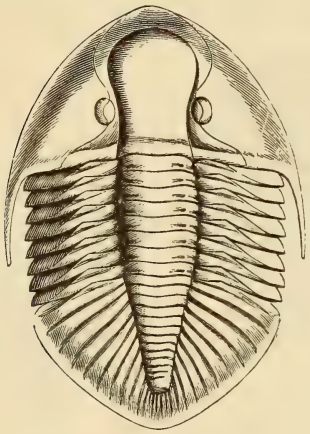

Fig. 373.—*Asaphus Canadensis* (Chapman). Ordovician.

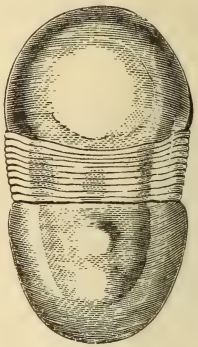

Fig. 374.—*Illænus Barriensis* (Murchison). Silurian.

or amalgamated with one another. Commonly, the pygidium is trilobed (fig. 373), like the thorax, and consists of a central elevated "axis" and of a marginal "limb." The limb is separated from the axis by axal furrows, and usually exhibits on its surface the lines which indicate the component pleuræ, as well as the longitudinal furrows on the faces of these. The extremity of the pygidium is sometimes simply rounded, with an "entire" margin; but it may be prolonged into a shorter or longer spine or "mucro" (fig. 369), and the ends of the pleuræ may also be extended into spine-like projections (fig. 375). The number of rings in the tail varies from two (*Sao hirsuta*) to twenty-eight (species of *Amphion*).

With regard to the condition of the *under* surface of the Trilobites, the progress of our knowledge has been slow, and is still in some respects far from complete. Specimens showing the inferior surface are exceedingly rare, and until of late years the only structure which had been detected on this aspect of the animal was the

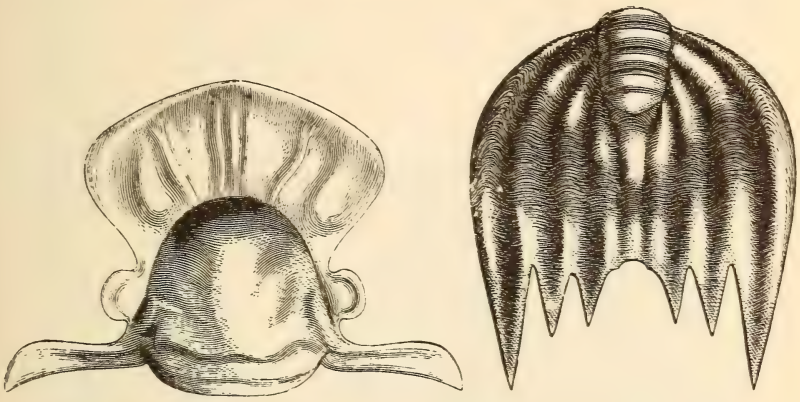

Fig. 375.—Glabella and pygidium of *Dikellocephalus magnificus*, Quebec group (Lower Ordovician). (After Billings.)

upper lip. The margin of the head-shield (as that of the pygidium also) is turned under in the form of a broader or narrower downward and inward inflection or "doublure" (fig. 377, *d*), and to the centre of this is attached the lip-plate or "hypostome." The form of this varies, but usually it is either an oval gibbous plate or it is broad and deeply forked behind (figs. 376, 377, *h*). Beside this lip-plate, in a specimen of *Asaphus platycephalus*, Dr Henry Woodward detected a jointed filament (fig. 376, *p*), apparently attached to a maxillary plate, and representing a "maxillary palpus." At a later period, Mr Billings described a specimen of *Asaphus platycephalus*, showing the under surface of the body, with a pair of apparently jointed appendages attached to each segment of the thorax; but the nature of these structures as ambulatory legs was not universally admitted. The correctness of the view held by Mr Billings as to the nature of the thoracic limbs in *Asaphus platycephalus* has, however, been completely established by a specimen of *Asaphus megistos*, from the Ordovician rocks of Ohio, which shows the under surface with its appen-

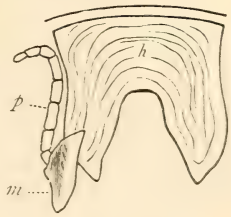

Fig. 376.—Buccal organs of *Asaphus platycephalus* (after Woodward). *h*, Hypostome; *p*, Palpus; *m*, Maxilla (?).

dages, and which has been described by Dr Mickleborough and Mr Walcott. In this remarkable specimen (fig. 377), all the segments of the thorax, as well as those of the pygidium, are provided with jointed limbs, while branchial filaments (*b*) are likewise present. Apart from the interesting specimens above noticed, the condition of the under surface of the Trilobites, with its appended structures, has been fully investigated by Mr Charles D. Walcott, whose researches have been carried on by the method of making thin transverse and longitudinal sections of rolled-up specimens. This able observer has shown that the visceral cavity of the Trilobites (fig. 378, *b*) was bounded inferiorly by a thin membrane, which was attached to the lower margin of the dorsal crust all round. This ventral membrane was supported by calcified arches, which in turn supported the appendages beneath. As to these latter, it is now established that there existed a row of articulated appendages on each side of the middle line below (fig. 379). In the genus *Calymene*, as will be seen from the accompanying illustrations, the thoracic appendages were in the form of slender, five-jointed legs, in which the terminal segment forms a pointed claw, and the basal segment carries a jointed appendage, regarded by Mr Walcott as homologous with the "epipodite" of many recent Crustaceans. On each side of the thoracic cavity there is, also, attached a row of bifid spiral appendages (fig. 378, *e*), of the nature of gills; and branchial appendages were probably attached to the bases of the

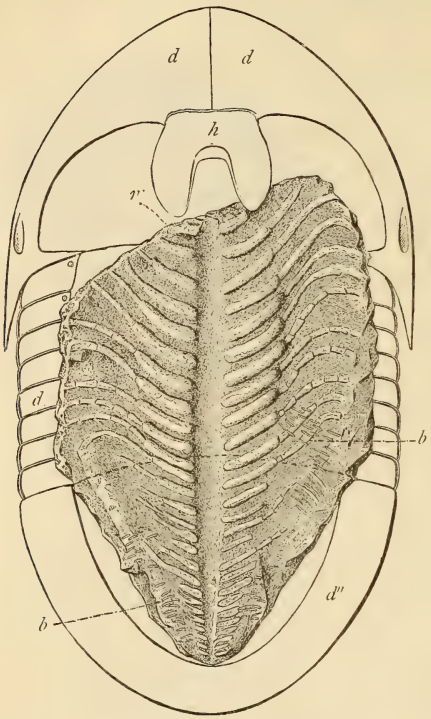

Fig. 377.—Under surface of the body of *Asaphus megistos*, from the Ordovician rocks of Ohio, with the missing parts restored in outline. *d*, and *d''*, Doublure or infolded margin of the cephalic shield, thorax, and pygidium respectively. All the rings of the thorax and tail carry jointed limbs, and branchial filaments (*b*) are also present. In front, the bases of the last pair of cephalic appendages (maxillipedes) is shown (*m*). *h*, The hypostome. (After Walcott.)

thoracic limbs as well. The abdominal or pygidial rings carried appendages also, a pair to each segment, but these do not appear to have differed in form from the thoracic limbs. With regard, finally, to the appendages of the head, the mouth is situated behind the hypostome, and is bounded by four pairs of jointed manducatory appendages, the basal joints of which are, partly or wholly, modified to act as jaws. The hindmost cephalic appendages (fig. 379, *b*) are larger than the anterior ones, and may be regarded as foot-jaws.

In connection with the exoskeleton of the Trilobites, a few words may be said as to the *minute* structure of the crust. Thin vertical sections (fig. 380, B) show that the crust is traversed by vertical canals or tubes of different sizes, the general tissue being finely

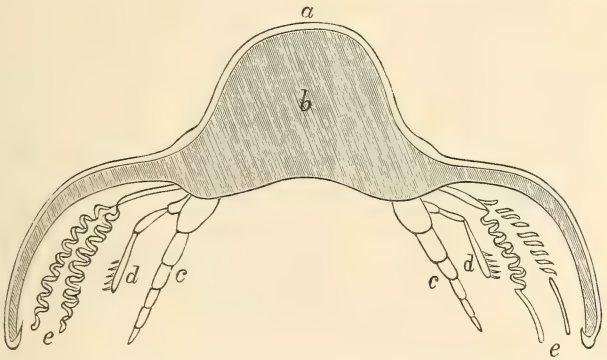

Fig. 378.—Transverse section of the thorax of *Calymene senaria*, partially restored (after C. D. Walcott). *a*, Dorsal crust; *b*, Visceral cavity, continued laterally to the pleural margins of the dorsal crust; *c*, Legs, restored; *d*, Epipodite; *e*, Spiral gills. Enlarged six times.

tubulated so as to resemble somewhat the dentine of teeth, and there being usually a system of comparatively large vertical tubes as well. Tangential sections (fig. 380, A and C) may only exhibit the openings of the larger set of tubes, or may show the minute and close-set apertures of the small tubuli as well. Where a large set of tubes is clearly developed, the minute structure of the crust is very similar to that of the shell of the recent *Limulus;* but the presence of these large tubes cannot be regarded as a distinctive feature, since similar canals are present in the shell of the Lobster, in parts at any rate.

With regard to the *development* of the Trilobites, the eggs have been noticed by both Barrande and Walcott. They are spheroidal or cylindroidal in shape, and mostly about a twenty-fifth to a fiftieth of an inch in diameter, and they seem to have been deposited in clusters. The larval condition of the Trilobites is only known in

certain cases, and it is possible that the young may often have been naked. This subject has been chiefly worked out by Barrande, who has shown that, so far as our present knowledge goes, the development of the Trilobites follows one or other of four principal lines. In one group of forms (*e.g.*, *Sao hirsuta*), the most minute larvæ observed possess a head-shield, but have no pygidium, while the thorax is either wanting or rudimentary. In another type (*Agnostus*), the larva has both the head-shield and pygidium in a developed condition, but the thorax is wanting. In a third, all the three regions of the body are present, but the thorax and pygidium are at first incomplete; and in a fourth group, though the thorax possesses the number of rings proper to the adult, the pygidium is imperfect.

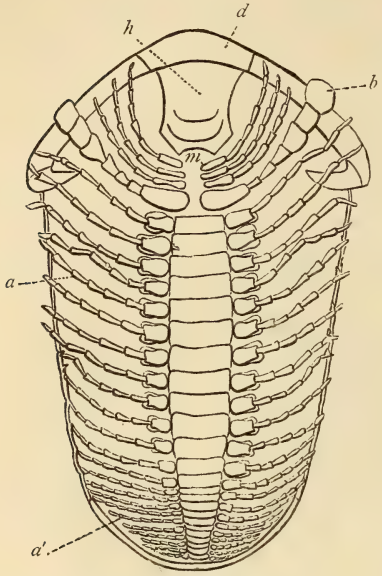

Fig. 379.—Restoration of the under surface of *Calymene Blumenbachii*, showing the appendages. *d*, Doublure of the cephalic shield; *h*, Hypostome; *b*, The last pair of cephalic appendages (maxillipedes); *m*, Mouth, bounded by the jaws; *a*, Thoracic limbs; *a'*, Abdominal limbs. (After Walcott.)

As to their *mode of life*, the Trilobites, as before remarked, seem to have delighted in muddy bottoms, though often found in limestones, and they must have frequented particular localities in vast numbers. In connection with this subject, we may briefly notice certain tracks or markings in the rocks, which may perhaps have been pro-

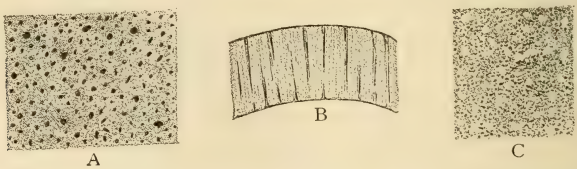

Fig. 380.—A, Tangential section of the crust of *Calymene senaria*, showing the openings of large and small tubes; B, Vertical section of the same; C, Tangential section of the crust of *Asaphus Canadensis*, showing a minutely porous structure. All the figures are greatly magnified. (Original.)

duced by these extraordinary extinct Crustaceans, or by their allies the King-crabs and Eurypterids. The most interesting of the tracks in question are those which have been described by Professor Owen from the Potsdam Sandstone (Upper Cambrian) of Canada, under the name of

Protichnites. The tracks upon which this genus is founded (fig. 381, A and B) consist essentially of a median groove, with a number of depressions or footprints on each side in corresponding pairs, these being often arranged in answering groups, of seven or eight pairs each. Sometimes the pits or footprints are replaced by shallow grooves, on each side of the main median groove (fig. 381, B). The tracks of *Protichnites* indicate the existence in the Upper Cambrian of some animal of very considerable size, since they are sometimes half a foot or more in width. That the animal producing these tracks was a Crustacean can hardly be doubted; the median groove being made by the tail-spine, and the lateral markings by the feet; and as we know that large Trilobites actually lived during this period, it seems most reasonable to suppose that we have in these the real makers of the tracks. Sir William Dawson, however, has shown that tracks of a closely similar nature are formed by the living

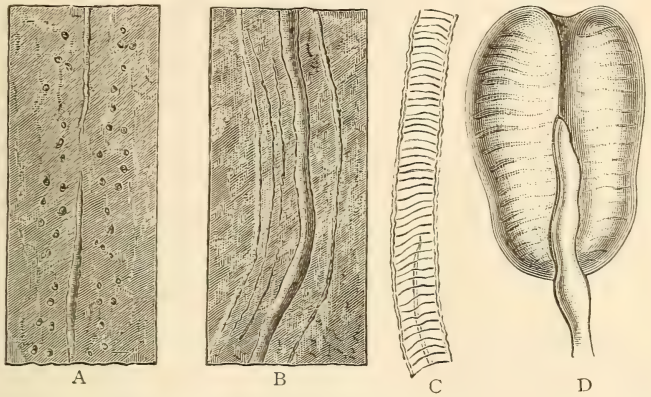

Fig. 381.—Supposed Crustacean tracks and burrows. A, Portion of the track of *Protichnites alternans*, from the Potsdam Sandstone, reduced to one-tenth of the natural size; B, Portion of the track of *Protichnites lineatus*, from the same formation, similarly reduced; C, Portion of *Climactichnites Wilsoni*, from the Potsdam group, reduced to one-thirtieth of the natural size; D, *Rusichnites* (*Rusophycus*) *bilobatus*, from the Clinton formation (Silurian), reduced one-half. (After Owen and Hall.)

King-crabs (*Limulus*), and he would therefore ascribe *Protichnites* rather to the Eurypterids. The same eminent observer has also shown that smaller forms of *Protichnites* occur in the Carboniferous; and he ascribes these to the Limuloid genus *Belinurus*. The curious track known as *Climactichnites* (fig. 381, C) is likewise found in the Potsdam formation, and consists of a band about six inches wide, crossed by straight ridges, and bounded by beaded margins. These were probably formed by the same animal as that which produced *Protichnites*, and Dawson has shown that the living *Limulus*, when it uses its swimming-feet, gives rise to a ladder-like track of the same kind. Prof. Chapman believes that both *Protichnites* and *Climactichnites* are really of vegetable origin. The only other fossil which need be mentioned in this connection is the curious *Rusichnites*, which is of common occurrence in the Ordovician and Silurian rocks of North America, and is also found in the Carboniferous. Originally described as a plant under the name of *Rusophycus*, its name was changed by Dawson to *Rusichnites*, in accordance with his belief that it really represents the *casts* of the bur-

rows of Trilobites, and that it can be shown to be sometimes connected with footprints consisting of a double series of transverse markings. In form, *Rusichnites* (fig. 381, D) presents itself as an oval, cylindroidal body, deeply furrowed, or bilobed, by means of a longitudinal sulcus, the lateral halves being transversely ridged or grooved. The body thus constituted may be independent, or may stand in apparent connection with a cylindrical and slender appendage.

With regard to their *systematic position*, the Trilobites have been usually regarded as Entomostracous Crustaceans, with relationships to the Phyllopods and to the *Merostomata;* but they have been sometimes considered as related to the Isopods. With regard to these last, there is no doubt a considerable general likeness between such an Isopod as *Serolis* and various forms of the Trilobites; and a tangible point of resemblance is found in the fact that in many Isopods the caudal segments coalesce to form a shield like the pygidium of the Trilobites. On the other hand, the segmentation of the body in the Trilobites is indefinite, the number of limbs is large, and thoracic branchiæ are developed; whereas in the Isopods the segmentation of the body is definite, there are only seven pairs of legs, and the branchiæ are abdominal. With the Phyllopods, the Trilobites are in agreement as regards the indefinite segmentation of the body; and the recent genus *Apus* possesses a lip-plate which in form is very similar to that of the Trilobites. The Trilobites, however, have a calcareous crust; their limbs are jointed, and not phyllopodous; and the segments of the abdomen are anchylosed. There are, finally, remarkable points of relationship between the Trilobites and the *Merostomata*, and particularly between the former and the Limuloid types of the latter. Thus, the Trilobites show affinities with the *Merostomata* in the possession of a very similar head-shield to that of the latter, the presence (particularly in some extinct Limuloids) of distinct indications of a "facial suture," the existence of compound sessile eyes, and the microscopic structure of the crust. Moreover, the larva of the recent *Limulus* (fig. 382) is destitute of the tail-spine of the adult, and in many respects shows a striking resemblance to certain of the Trilobites, and particularly to the genus *Trinucleus*. There are, however, various striking points of difference between the Trilobites and the Limuloids. Thus the former always possess free thoracic segments, and the appendages carried on these differ en-

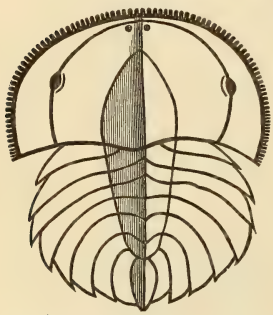

Fig. 382.—Larva of *Limulus* on hatching, greatly enlarged. (After Dohrn.)

tirely from those borne on the same region in any of the *Merostomata*. Again, the Trilobites have no "ocelli," and have a well-developed hypostome. On the other hand, the thoracic somites in the Limuloids may be completely anchylosed (as they are in *Limulus* itself); ocelli are present as well as compound eyes; and the hypostome is rudimentary or absent. Upon the whole, in spite of the above-mentioned differences, it would seem that the Trilobites are more nearly related to the *Merostomata* than to any other group of the *Crustacea*, and if, as maintained by Claus and other high authorities, the latter are properly referable to the *Arachnida*, it will be apparently necessary to transfer the *Trilobita* also to this class of the *Arthropoda*. Apart, however, from the difficult question as to whether the Limuloids and Eurypterids are referable to the *Arachnida* or to the *Crustacea*, it may be questioned if there is sufficient justification, in the present state of our knowledge, for placing these two groups along with the Trilobites in the common division to which Claus has given the name of *Gigantostraca*. The differences between the *Trilobita* on the one hand, and the *Xiphosura* and *Eurypterida* on the other hand, are, at any rate, so numerous that it would be a matter of difficulty to frame a definition of the *Gigantostraca* which would embrace these three orders, and would at the same time exclude all the other groups of the *Crustacea*.

The general facts as to the *distribution* of the *Trilobita* in past time are soon told. The Trilobites are exclusively Palæozoic, their range extending from the Upper Cambrian to the Permian. If the problematical *Palæopyge Ramsayi* of the Longmynd beds be a Trilobite, then the order has its commencement in the Lower Cambrian. In the Upper Cambrian rocks the order attained a wonderful development, the number of generic and specific types already known from this formation being very large, while individuals are sometimes extremely abundant. Some of these so-called "Primordial" Trilobites attain a very great size, being only surpassed amongst later forms by some species of *Asaphus*. They mostly belong to the families of the *Agnostidæ*, *Conocephalidæ*, and *Paradoxidæ*, and to the genera *Paradoxides*, *Conocoryphe*, *Sao*, *Ellipsocephalus*, *Hydrocephalus*, *Arionellus*, *Dikellocephalus*, &c. Along with these, however, are genera such as *Agnostus*, which pass up into the Ordovician. Some of the "Primordial" Trilobites are not so highly organised as their successors, as shown by the occasional absence of eyes, or want of the facial suture, by the imperfect segmentation of the glabella, or by the multiplication or diminution of the number of the body-rings; but others do not exhibit any inferiority to those of later periods.

In the Ordovician and Silurian rocks the Trilobites attain their

maximum of development, the leading families being the *Asaphidæ*, *Phacopidæ*, *Trinucleidæ*, *Cheiruridæ*, and *Calymenidæ*, and the chief genera being *Asaphus*, *Ogygia*, *Phacops*, *Trinucleus*, *Ampyx*, *Cheirurus*, *Encrinurus*, *Calymene*, and *Homalonotus*. In the Devonian rocks, again, Trilobites are tolerably abundant, though less so than in the preceding series. The commonest Devonian genera are *Phacops*, *Homalonotus*, *Proetus*, and *Bronteus*. Lastly, the order seems to die out before the close of the Palæozoic epoch, being represented in the Carboniferous period solely by the four genera *Phillipsia*, *Brachymetopus*, *Griffithides*, and *Proetus;* while in the Permian rocks only a single species of *Phillipsia* has hitherto been detected.

In the following, a brief summary of the families of the *Trilobita*, indicating the principal genera of each, and their distribution in time, will be given. No strictly zoological arrangement of these families is as yet possible, except in a general sense, but the classification proposed by M. Barrande, one of the most illustrious palæontologists of this century, has been in the main adhered to.

Fig. 383.—*Harpes ungula*, from the Silurian of Bohemia. (After Barrande.)

Family 1. Harpedidæ.—Cephalic shield large, and horse-shoe-shaped, its posterior angles greatly prolonged, and its margin or "limb" perforated by pores (fig. 383). The glabella is conical and prominent, with slightly marked furrows, and the eyes are small, and consist of a few lenses. There are from twenty-five to twenty-nine thoracic segments, and the pygidium is extremely small, and consists of three or four amalgamated segments. The species of *Harpes*, the sole genus comprised in this family, are principally Ordovician and Silurian, but a few Devonian forms are known.

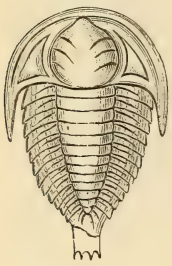

Fig. 384.—*Remopleurides radians*. Ordovician. (After Barrande.)

Family 2. Remopleuridæ.—In this family the head is greatly developed, semicircular in shape, the genal angles produced into spines. The glabella is smooth, or possesses three pairs of lateral grooves, and the facial sutures unite in front of it. The eyes are very long and are reticulated. There are eleven to thirteen body-rings, with grooved pleuræ, and the pygidium is very small, and is often reduced to two segments. This family contains only the single genus *Remopleurides* (fig. 384), which is confined to the Ordovician and Silurian deposits.

Family 3. Paradoxidæ or Olenidæ.—Head-shield well developed, crescentic, the genal angles produced. The glabella, typically, widest anteriorly, with well-marked grooves. The facial

sutures nearly parallel, cutting the head-shield separately; the eyes large. The body is very long (fig. 385, *a*); the thorax has from twelve to twenty segments, with grooved pleuræ; the pygidium being usually small and of few segments. The family is essentially characteristic of the Cambrian deposits, ranging through all the divisions of this formation.

The principal genus of this group is *Paradoxides* itself (fig. 385, *a*, and fig. 386), with its long and trilobed body, sometimes reaching a length of two feet or more. The thorax in this genus is greatly

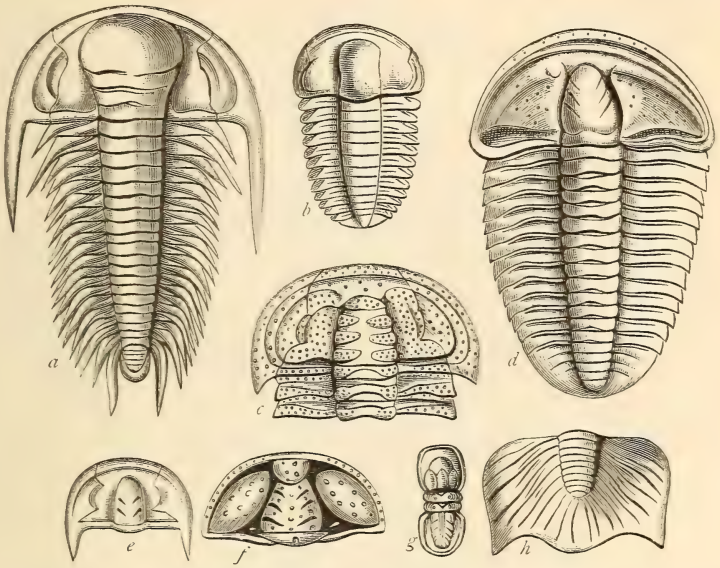

Fig. 385.—*Paradoxidæ* and *Conocephalidæ*. *a*, *Paradoxides Bohemicus*, reduced in size; *b*, *Ellipsocephalus Hoffi*; *c*, *Sao hirsuta*; *d*, *Conocoryphe Sultzeri*—(all the above, together with fig. *g*, are from the Upper Cambrian or "Primordial Zone" of Bohemia); *e*, Head-shield of *Dikellocephalus Celticus*, from the Lingula Flags of Wales; *f*, Head-shield of *Conocoryphe Matthewi*, from the Upper Cambrian (Acadian Group) of New Brunswick; *g*, *Agnostus rex*, Bohemia; *h*, Tail-shield of *Dikellocephalus Minnesotensis*, from the Upper Cambrian (Potsdam Sandstone) of Minnesota. (After Barrande, Dawson, Salter, and Dale Owen.)

elongated, and consists of sixteen or twenty rings, while the axis of the pygidium often contains two segments only. The eyes are long, reniform, and smooth. The genus is characteristic of, and confined to, the Cambrian period. *Plutonia* and *Anopolenus*, with a similar geological range, are closely related to *Paradoxides;* but the former of these two genera has a narrow glabella and a tuberculated surface, while the latter has the last two pleuræ of the thorax dilated and bent backwards, and the pygidium has wide lateral lobes. The genus *Olenellus* resembles *Paradoxides* in most respects, but

there are only thirteen or fourteen segments in the thorax, and the lateral lobes of the pygidium are undeveloped, the elongated and pointed axis alone remaining. The genus *Olenellus* appears to be characteristic of the Lower Cambrian deposits, while *Paradoxides* distinguishes the Middle Cambrian fauna, and *Olenus* (or *Dikellocephalus*) the Upper Cambrian.

In *Hydrocephalus*, again, the glabella is immensely inflated, with a median longitudinal groove; and the facial sutures cut the outer

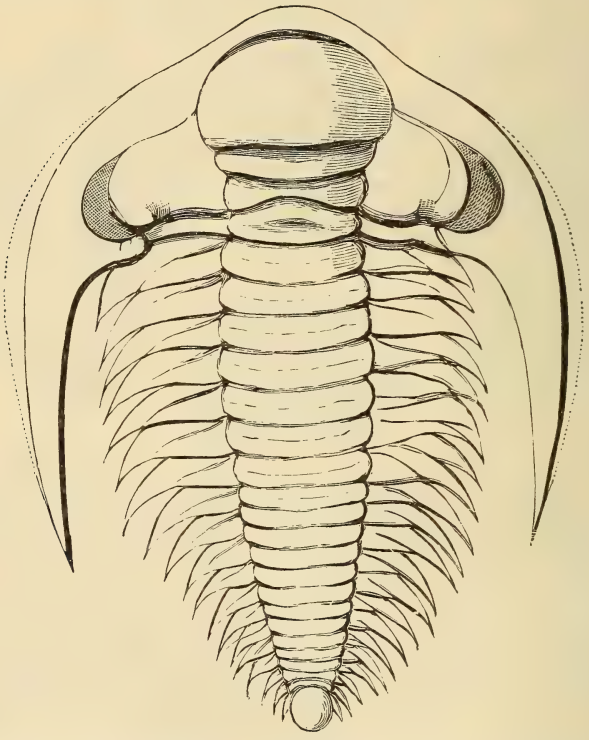

Fig. 386.—*Paradoxides Micmac.* St John's Group (Cambrian), Newfoundland. (After Dawson.)

margins of the head-shield, so that the free cheeks become much reduced in size, and the genal spines are attached to the fixed cheeks. Eyes are wanting, and there are only twelve body-rings. A more important and widely distributed genus of this family is *Olenus* (fig. 387), in which the general characters are very similar to those of *Paradoxides*, but the glabella is contracted in front so as to become conical, and its furrows are often extended completely

across it: there are only fourteen body-rings; and the pygidium is well developed. *Parabolina* includes *Oleni* with only twelve body-rings, and with a spined margin to the pygidium; while *Peltura* embraces forms in which the hinder angles of the head-shield are rounded, and the glabella is prolonged forwards to the front margin. *Olenus* and its sub-genera are confined to the Cambrian period, and specially distinguish the Upper Cambrian desposits. Characteristic of the same geological horizon is the genus *Dikellocephalus* (figs. 375, and 385, *h*) in which the most striking feature is the broad, fanlike, often spined tail, with its short many-ringed axis. The facial sutures cut the margin of the head-shield separately in front, and the grooves of the glabella are like those of many *Oleni* in joining from side to side.

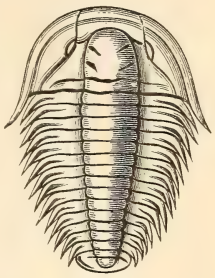

Fig. 387.—*Olenus micrurus*, from the Upper Cambrian. (After Salter.)

Family 4. CONOCEPHALIDÆ.—This family is a convenient one to retain, though it does not seem at present possible to separate it from the preceding by any rigid definition. Its members resemble the *Paradoxidæ* in general characters, but the glabella is narrow in front, or, at any rate, not dilated in this region, and the tail is usually fairly well developed, while the thoracic rings are not so numerous as in the typical forms of the latter. Moreover, most of the members of the *Conocephalidæ* have the power of rolling up into a ball. The type-genus is *Conocoryphe* or *Conocephalites* (fig. 385, *d* and *f*), which has resemblances to both *Olenus* and *Calymene*, its glabella approaching that of the latter in its comparatively great posterior width and its contraction in front. Eyes are usually, but not always present; the facial sutures are discontinuous; the fixed cheeks are large and the free cheeks small; and there are fourteen or fifteen body-rings, while the tail has from two to eight rings. The genus is represented by very numerous species in the Upper Cambrian, and also occurs in the Ordovician rocks. *Ellipsocephalus* (fig. 385, *b*) is related to the preceding, but the glabella is subquadrate, smooth, and convex, and there are twelve to fourteen body-rings. *Angelina* (fig. 388) is another Upper Cambrian genus, with affinities to *Olenus*. Its glabella, however, is destitute of grooves, and the tail is composed of four or five rings, while the body-segments are fifteen in number. The genus *Sao* (fig. 385, *c*), of the same formation, is a link between the present family and the *Paradoxidæ*. It is distinguished by its prominent furrowed glabella, the possession of seventeen body-rings, and the minute tail of two segments only. *Arionellus*, also Cambrian, has sixteen body-rings, and three caudal segments; and the allied genus *Menocephalus*, of

the same age, is chiefly separated from the former by its much more convex glabella. Lastly, *Bathyurus* (Upper Cambrian and Ordovician) and *Bathyurellus* (Ordovician) form in some respects intermediate types between the *Conocephalidæ* and the *Asaphidæ;* and the Olenoid genus *Triarthrus* survives to near the middle of the Ordovician period.

Family 5. BOHEMILLIDÆ.—This family contains only the Ordovician genus *Bohemilla*, characterised by its greatly developed head; the glabella being of large proportionate size, with four pairs of lateral grooves, the hinder ones of which pass completely from side to side, so as to divide this region of the head into regular rings or

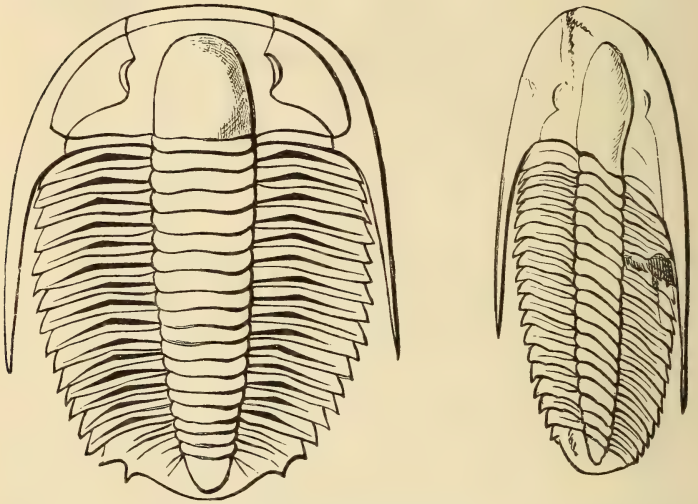

Fig. 388.—*Angelina Sedgwickii*, in its natural condition, and distorted by cleavage. Upper Cambrian. (After Salter.)

segments, closely resembling those of the thoracic axis. The eyes are large and reticulated; the course of the facial sutures is unknown; the genal angles are prolonged into long spines, directed transversely rather than backwards; and the thorax and pygidium are not clearly marked off from one another, the former consisting apparently of five segments and the latter of two.

Family 6. CALYMENIDÆ.—In this family the crust is often tuberculated or granulated; the head is well developed; the glabella is widest behind; and the facial sutures are discontinuous, and terminate at the posterior angles of the cephalic shield. There are thirteen segments in the thorax, with grooved pleuræ; the tail is of moderate size; and the condition of the eyes is variable. In

Calymene itself (fig. 372) the head is usually crescentic, with rounded genal angles; and the glabella is conical, strongly convex, with deep axal furrows, and divided by three deep lateral grooves on each side, all the "lobes" thus formed being globose, and the hindmost being the largest. The eyes are minute and reticulated, but are rarely recognisable. The tail is convex, with a well-marked axis, and the hypostome is quadrate and forked posteriorly. The animal possessed in perfection the power of rolling up into a ball, specimens commonly occurring in this condition. The species of *Calymene* are principally Ordovician and Silurian, and the three most familiar species are the nearly allied *C. Blumenbachii*, *C. senaria*, and *C. brevicapitata*. The genus is also known to have survived, in North America, into the commencement of the Devonian period.

The genus *Homalonotus* is the only other member of the *Calymenidæ*, and is distinguished from *Calymene* by the greatly elongated and faintly trilobed body (fig. 389). The glabella, further, is smooth or exhibits but faint traces of lobation. The species of *Homalonotus* are Silurian and Devonian, and the genus has a wide distribution in space. A very familiar species is the *Homalonotus delphinocephalus* of the Silurian rocks.

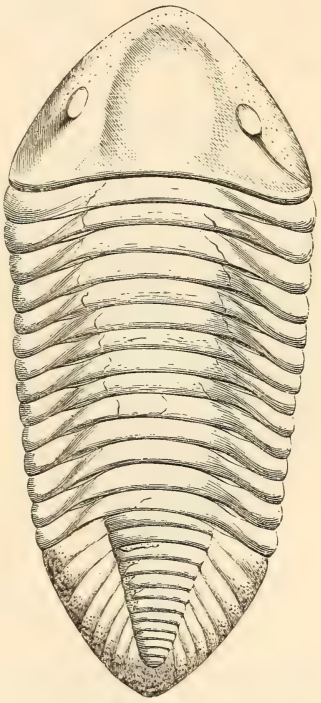

Fig. 389.— *Homalonotus delphinocephalus*. Silurian.

Family 7. ASAPHIDÆ. — Large Trilobites, generally oval, and never furnished with spines or tubercles on their surface. The eyes smooth, and the facial sutures terminating on the posterior margin. The cephalic and caudal shields generally of large size, the glabella of the former often obscure, and the latter sometimes exhibiting no indication of its component segments. The body-rings usually eight in number, with grooved pleuræ. The family is characteristically Ordovician, and the two principal genera are *Asaphus* and *Ogygia*. In the genus *Asaphus* (figs. 390, 392, 393) the general trilobation is somewhat indistinct, and the caudal shield is generally equal to the head in size. The genal angles of the head-

shield may be rounded or spinose, and the glabella is not marked off by conspicuous axal furrows. The facial sutures are discontinuous, the eyes crescentic, the hypostome deeply forked, and the pygidium may or may not show a conspicuous axis, its hinder extremity being usually rounded, and its margin always entire. This important genus is characteristic of the Ordovician rocks, and the species have a world-wide distribution, some of the forms attaining the extraordinary size of two feet in length. The genus *Asaphus* has been divided into a number of sub-genera, of which *Isotelus* and *Megalaspis* are the most important. In the former of these (fig. 392) the axis is very wide, the glabella is imperfectly marked off,

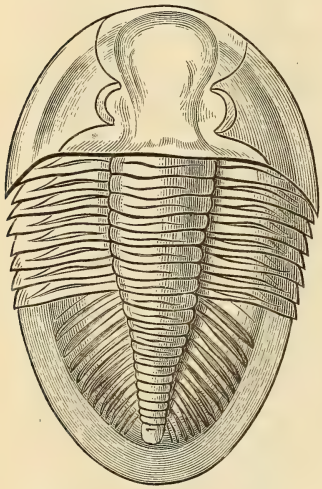

Fig. 390.—*Asaphus tyrannus.* Ordovician. (After Salter.)

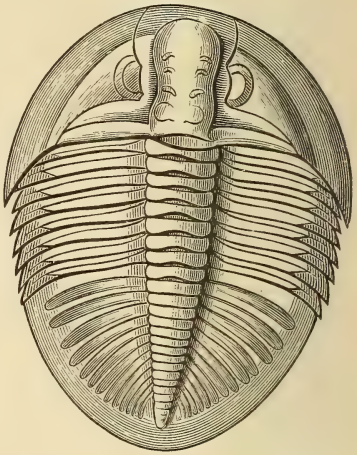

Fig. 391.—*Ogygia Buchii.* Ordovician. (After Salter.)

and the pleuræ have rounded ends. In *Megalaspis* (fig. 393), on the other hand, the axis is narrow, the glabella is very short, and the head-shield is usually greatly extended in front.

The genus *Ogygia* is closely allied to *Asaphus* in general form and proportions; but the axis of the pygidium is more conspicuously marked than in most *Asaphi* (fig. 391), the hypostome is *rounded* and not cleft, the glabella is distinctly furrowed, and the pleuræ of the thoracic segments have only rudimentary "fulcra." The species of *Ogygia* are confined to the Ordovician rocks. This is also the case with the genus *Niobe*, which is in some respects intermediate between *Asaphus* and *Ogygia*, having the round hypostome and lobed glabella of the latter, while it approaches the former in its wide glabella and its obtuse and faceted pleuræ. The Ordovician

genus *Stygina* is related to *Ogygia*, but the head-shield and pygidium are very similar. Lastly, the Upper Cambrian genus *Psilocephalus* forms a link between *Asaphus* and *Illænus;* while the genus *Nileus* might be almost indifferently placed with either the *Asaphidæ* or the *Illænidæ*.

Family 8. Illænidæ.—In this family the head and tail are greatly developed, and, as in the *Asaphidæ*, are approximately equal in size (fig. 394). The glabella is broad and rounded, destitute of lobes, and with the axal furrows hardly at all marked. There are eight to

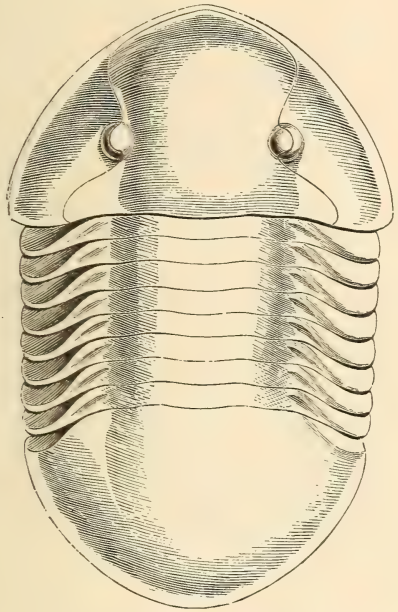

Fig. 392.—*Asaphus* (*Isotelus*) *platycephalus*. Ordovician.

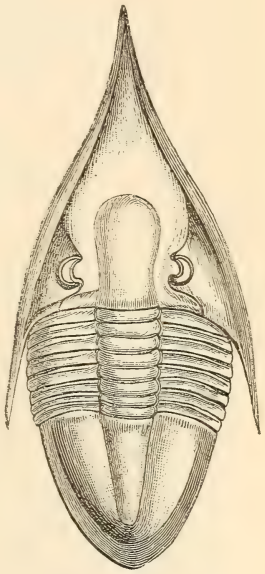

Fig. 393.—*Asaphus* (*Megalaspis*) *extenuatus*, of the natural size. Ordovician, Sweden. (After Angelin.)

ten body-rings; and the axis of the tail is truncated or wanting, and in no case exhibits definite segmentation. The free cheeks are extremely small; the facial sutures are separate; and the eyes are crescentic.

If *Nileus* be regarded as belonging to the *Asaphidæ*, the only well-defined genus in this family is *Illænus* itself (fig. 394). In this genus the head is large, convex, and tumid, as is also the tail, the glabella and pygidial axis being hardly marked out, and being wholly unsegmented. In the typical forms of this group (*Illænus* proper), the axis of the thorax is not disproportionately wide, and

the axal furrows are distinct; but in others (*Bumastus*), the thoracic axis is extremely wide, and is hardly separated from the pleuræ by

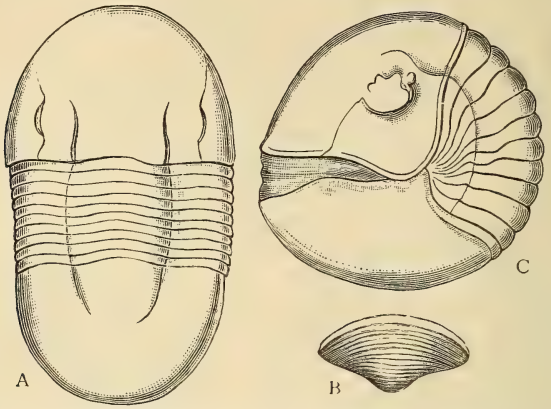

Fig. 394.—A, A complete example of *Illænus Davisii*, in its unrolled state—Ordovician; B, Hypostome of the same; C, *Illænus* (*Bumastus*) *Barriensis*, rolled up—Silurian. (After Salter.)

recognisable axal furrows (fig. 374). In the former of these sections there are ten body-rings; whereas in *Octillænus* and *Panderia* there

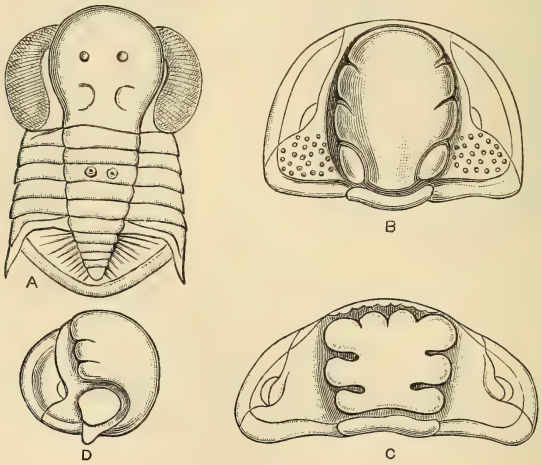

Fig. 395.—A, *Æglina prisca*—Ordovician; B, Head-shield of *Cheirurus juvenis*—Ordovician; C, Head-shield of *Amphion Fischeri*—Ordovician; D, Side view of the head-shield of *Sphærexochus mirus*—Ordovician and Silurian. (After Barrande and Salter.)

are only eight body-rings, and in *Dysplanus* there are nine. The species of *Illænus* are exclusively confined to the Ordovician and Silurian periods.

Family 9. Æglinidæ.—This family contains only the single genus *Æglina* (fig. 395, A), of the Ordovician rocks, and is chiefly distinguished from the preceding by the much larger size of the eyes, and the smaller number of body-rings. The head and tail are both of large size, the latter with a truncated axis; the glabella is not conspicuously marked out; the facial sutures are discontinuous; and the eyes are extremely large and reticulate; while the segments of the thorax are reduced to five or six in number.

Family 10. Cheiruridæ.—In this large and important family the head-shield is well developed, with discontinuous facial sutures, which terminate on its outer margin. The glabella is usually highly convex or tumid, with well-marked axal furrows and lateral grooves. There are ten to twelve, rarely fifteen or eighteen, generally eleven, body-rings, and the pygidium is small, of from three to five segments, the pleuræ terminating in free ends. The family ranges from the Upper Cambrian to the Devonian, but is principally characteristic of the Ordovician and Silurian rocks. In *Cheirurus* itself (figs. 395, B, and 396) the head is semicircular, with rounded or pointed genal angles, and with a strongly-arched glabella, which is deeply grooved by the lateral furrows. There are generally eleven body-rings, with ridged or slightly grooved pleuræ; and the tail has a well-marked axis of four rings, its pleuræ being prolonged into points or spines. *Amphion* (fig. 395, C) is nearly related to *Cheirurus*, but has from fifteen to eighteen body-rings, and exhibits minor differences as well. *Placoparia*, again, agrees with *Cheirurus* in having eleven body-rings, and also in the form and lobation of the glabella, but it is destitute of both eyes and facial sutures, as is also the genus *Areia*. *Sphærexochus*, lastly (fig. 395, D), while agreeing with *Cheirurus* generally, is distinguished by the extreme inflation of the glabella, and the presence of no more than three segments in the pygidium; while the basal lobes of the glabella are completely isolated, and there are only ten body-rings. We may also place here the very singular and aberrant genera *Staurocephalus* and *Deiphon*. In the former of these the general characters correspond with those of *Cheirurus*, but the anterior or "frontal" portion of the glabella is enormously swollen, and forms a great globular projection in advance of the line of the cheeks. The species of *Staurocephalus* are Ordovician and Silurian. In the

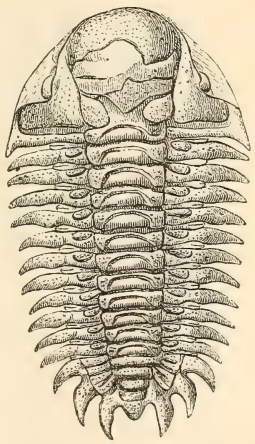

Fig. 396.—*Cheirurus insignis*, from the Silurian rocks of Bohemia. (After Barrande.)

still more curious *Deiphon*, of the Silurian rocks, the fixed cheeks are rudimentary, and are reduced to two curved spines, which spring from the sides of the swollen glabella, and carry the faceted eyes, while the free cheeks are obsolete. The axis of the tail is formed of four or five rings, and the pleuræ are prolonged into two spines on each side, one of these being formed by the first segment only, while the other, and much larger, one is made up of the amalgamated extremities of the remaining segments.

Family 11. Encrinuridæ. — This family is confined to the Ordovician and Silurian periods, and is related to the preceding through the intervention of *Amphion*. The head is fairly devel-

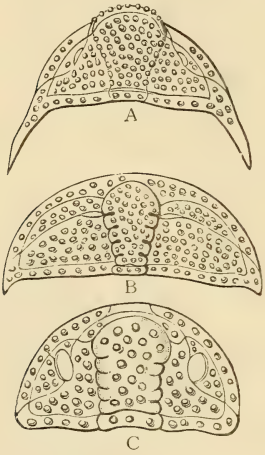

Fig. 397.—A, Head-shield of *Encrinurus punctatus* — Silurian; B, Head-shield of *Cromus intercostatus*—Silurian; C, Head-shield of *Cybele bellatula* — Ordovician. (After Barrande.)

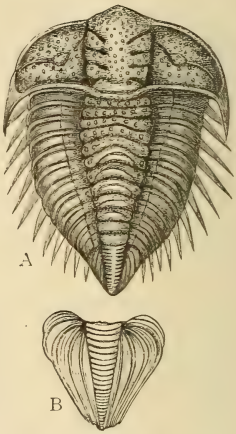

Fig. 398.—A, *Cybele Loveni*, of the natural size; B, Cast of the pygidium of *Cybele verrucosa*, enlarged twice. From the Ordovician rocks of Girvan. (After R. Etheridge, jun., and the Author.)

oped, the genal angles rounded or pointed, and the facial sutures discontinuous, and cutting the outer angles of the cephalic buckler. Eyes are present, though not of large size, and the glabella may or may not exhibit distinct lateral grooves. The surface is tuberculated, and some or all of the body-rings may bear spines. The thorax generally consists of eleven segments; and the tail, though moderate in size, has a well-marked axis, which is composed of very numerous rings.

In *Encrinurus* (fig. 397, A) the glabella is pyriform, strongly tuberculated, with the lateral furrows almost obsolete. The body-rings are eleven in number, and the axis of the pygidium is composed of extremely numerous rings. In this genus, as in its near

ally *Cybele*, the pygidium is long and triangular, and has its pleuræ bent backwards so as ultimately to become parallel with the axis (fig. 398, B). The range of the genus *Encrinurus* is principally Silurian, but the genus likewise occurs in the higher portion of the Ordovician series. The genus *Cybele* (= *Zethus*, Volborth) is distinguished from *Encrinurus* chiefly by its clavate glabella (fig. 397, C) and its possession of twelve body-rings, which are usually produced into spines (fig. 398, A). The facial sutures cut the margin of the head-shield close to the genal spines, and the tail resembles that of *Encrinurus* in form. The genus is characteristic of the Ordovician rocks. Lastly, in the Silurian genus *Cromus* (fig. 397, B) the glabella has four well-marked lateral grooves; the eyes are small and ovoid; and the pygidium looks like a continuation of the thorax, its axis being composed of from twelve to twenty-eight rings, and its pleuræ terminating in free points.

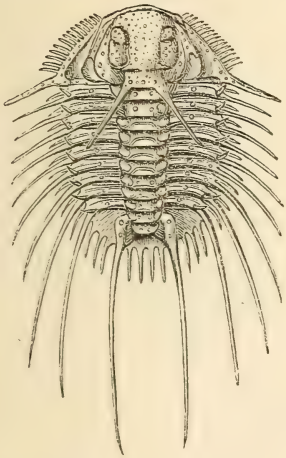

Fig. 399.—*Acidaspis Dufrénoyi*, from the Silurian rocks of Bohemia. (After Barrand—Copied from Zittel.)

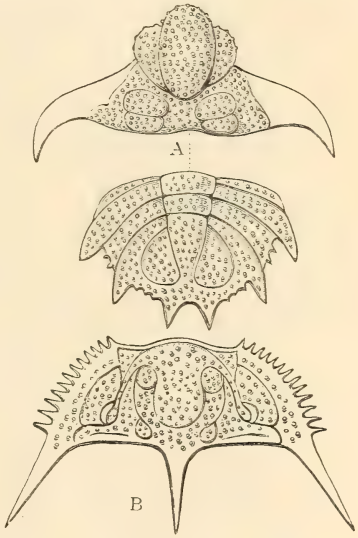

Fig. 400.—A, Head-shield and tail of *Lichas palmata*; B, Head-shield of *Acidaspis Hoernesi*. Silurian rocks of Bohemia. (After Barrande.)

FAMILY 12. DINDYMENIDÆ.—In *Dindymene*, of the Ordovician formation, the only genus which can be certainly referred to this family, the head-shield is semicircular, with a tumid glabella, destitute of lateral grooves. There are no eyes, nor facial sutures; and the cheeks are tumid, as in *Trinucleus*. There are ten body-rings, and the tail is large and distinctly segmented.

Family 13. Acidaspidæ.—Like the preceding, this family contains only a single genus—viz., *Acidaspis* itself. In this characteristically Silurian type (fig. 400, B), the usual form of the head-shield in the Trilobites is somewhat masked, the trilobation being rendered indistinct by the presence of an additional and secondary pair of axal furrows, which mark off a central inflated portion of the glabella. The thorax has nine or ten rings, with ridged pleuræ, which are terminated by spines; while the tail is very small, and has its margin fringed with spines (fig. 399). The facial sutures are continuous, or are sometimes wanting; and the eyes are of small size and smooth. The species of *Acidaspis* are found in the Silurian and Devonian rocks, and are usually readily recognised by their highly ornamented and spinose crust.

Family 14. Lichadæ.—The principal or only genus in this family is *Lichas*[1] itself (fig. 400, A), in which the body is broad and oval, and the crust is superficially more or less granulated or tuberculated. The head-shield is transversely elongated and very convex, and the glabella as a rule is not very clearly separated from the cheeks. The frontal grooves of the glabella are extended backwards, so as to enclose a central lobe. The facial sutures cut the anterior margin separately, and the eyes are small and smooth. There are nine or ten thoracic rings, with grooved pleuræ; and the pygidium is larger than the head, and often presents prominent spinose ends to its component rings. The species of *Lichas* are Ordovician, Silurian, and Devonian.

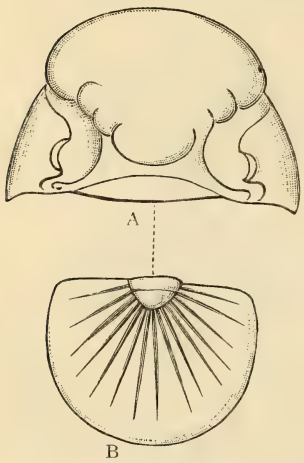

Fig. 401.—A, Head-shield of *Bronteus campanifer*, from the Silurian rocks of Bohemia; B, Tail of the same. (After Barrande.)

Family 15. Bronteidæ. — This family includes only the genus *Bronteus*, the species of which are found in the Ordovician, Silurian, and Devonian rocks. In this well-marked type (fig. 401) the body is broad, and could be rolled up, both the head-shield and the pygidium being of great size. The tail is particularly large, and is always more or less fan-shaped, the axis being short and rudimentary, while the "limb" is greatly developed. The head-shield is trilobed, the glabella being dilated in front, the

[1] The genus *Lichas* has been very fully treated of by Magister Friedrich Schmidt ('Revision der Ostbaltischen Silurischen Trilobiten,' Abth. II., 1885), by whom it has been split up into a number of sub-generic groups.

facial sutures being separate, and the eyes sickle-shaped. There are ten thoracic segments, and the pleuræ are ridged.

Family 16. Phacopidæ.—In this, one of the best-marked and most typical of the families of the Trilobites, the head is well developed, the glabella conspicuously broadest in front, with three or four lateral grooves, and the facial sutures united in front of the glabella, and cutting the outer margins of the cephalic buckler behind. The eyes are usually large, and are faceted (fig. 403); there are eleven body-rings, with grooved pleuræ; and the condition of the pygidium is variable. The hypostome is convex, and more or less

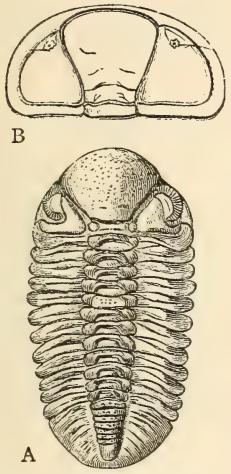

Fig. 402.—A, *Phacops Sternbergi*, from the Silurian rocks of Bohemia; B, Head-shield of *Phacops* (*Trimerocephalus*) *Volborthi*, Silurian, Bohemia. (After Barrande. Copied from Zittel.)

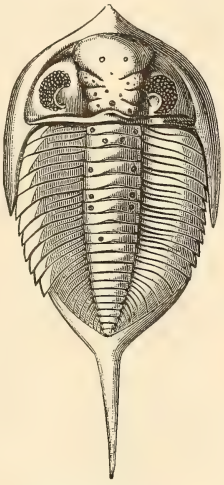

Fig. 403.—*Phacops* (*Dalmanites*) *longicaudata*. Silurian (Wenlock) of Britain and North America.

triangular in shape. The genus *Phacops* itself (with the sub-genera *Trimerocephalus*, *Phacops* proper, *Acaste*, *Pterygometopus*, *Chasmops*, *Dalmanites*, and *Cryphæus*) constitutes the entire family, and ranges from low down in the Ordovician series to the Upper Devonian rocks.

As regards the sub-genera of *Phacops*, *Trimerocephalus* includes Silurian and Devonian forms, in which the glabella is tumid in front (fig. 402, B); the glabella-furrows are faint or wanting; and the pygidium is of small size. In *Phacops* proper (fig. 402, A) the genal angles of the head-shield are rounded; the two anterior pairs of glabella-furrows are inconspicuous, and the glabella is very wide in front; the pleuræ are rounded; and the pygidium is of few segments, with an entire margin.

The species included under this head are Silurian and Devonian. *Dalmanites* (or *Dalmania*) includes forms with the pleuræ pointed and bent backwards, the pygidium being conspicuously segmented, and often ending in a spine (fig. 403). There are three glabella-furrows on each side, and the genal angles of the head-shield are long and produced. The species of this group are principally Silurian, but some of the forms are Ordovician and others are Devonian. *Chasmops* includes Ordovician species in which the genal angles are produced; the anterior glabella-lobes are laterally extended; the pleuræ have truncated ends; and the pygidium is of large size. *Pterygometopus* also includes Ordovician species, in which the frontal lobes of the glabella are laterally extended, and are intersected by the facial sutures. In *Acaste* are comprised Ordovician and Silurian species in which the glabella is not tumid, and exhibits all its furrows in a well-developed form, while the pygidium is often pointed. Lastly, *Cryphæus* includes Devonian types, and is principally distinguished by the fact that the margin of the pygidium is toothed or serrated.

Family 17. Proetidæ.—In this family the body is oval, distinctly trilobed, and capable of being rolled up. The head is of variable size, semicircular, sometimes with rounded, sometimes with spinose genal angles. The glabella is distinctly marked off from the cheeks, and the hindmost pair of glabella-furrows commonly circumscribe a basal lobe. The facial sutures cut the anterior margin of the head-shield separately. There are from eight to twenty-two body-rings, with grooved pleuræ, and the pygidium is distinctly segmented, and usually has an entire margin. The eyes have distinct facets, but are covered by a smooth cornea.

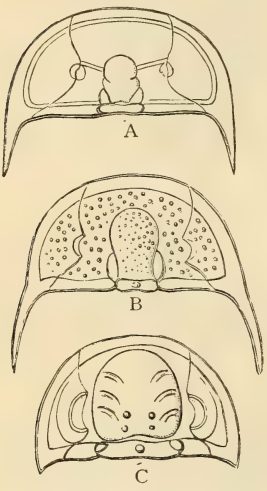

Fig. 404.—A, Head-shield of *Arethusina Koninckı*; B, Head-shield of *Cyphaspis Burmeisteri*; C, Head-shield of *Proetus Bohemicus*. From the Silurian rocks of Bohemia. (After Barrande.)

In *Proetus* itself (fig. 404, C) the head-shield is semicircular; the glabella has three pairs of lateral furrows; the eyes are large, semicircular, of numerous facets, covered by a thin cornea; there are eight or ten body-rings, and the tail has an "entire" border. The genus ranges from the Ordovician to the Carboniferous. *Cyphaspis* (fig. 404, B), of the Ordovician, Silurian, and Devonian rocks, differs from the preceding chiefly in its more convex glabella, with circumscribed basal lobes, its ovoid and remote eyes, and the generally greater number (fifteen to seventeen) of the body-rings. *Arethusina* (fig. 404, A), with a similar range in time, has its glabella much shortened, while the body-rings are as

many as twenty-two in number. *Carmon* is an Ordovician genus allied to *Proetus*, but it has neither eyes nor facial sutures, and it possesses eleven body-rings. The genus *Harpides* (apparently = *Erinnys* of Salter) is an interesting type, which appears to be intermediate between the *Proetidæ* and *Olenidæ*, and which carries back the range of the former into the Upper Cambrian. It has the "limb" of the head-shield very wide, and covered with a network of radiating and bifurcated nervures. On the other hand, the *Proetidæ* are represented in the Carboniferous rocks, not only by *Proetus* itself, but also by the genera *Phillipsia*, *Griffithides*, and *Brachymetopus*, one species of the first of these genera having been detected in deposits of Permian age. These types are therefore the most modern examples of the order *Trilobita* at present

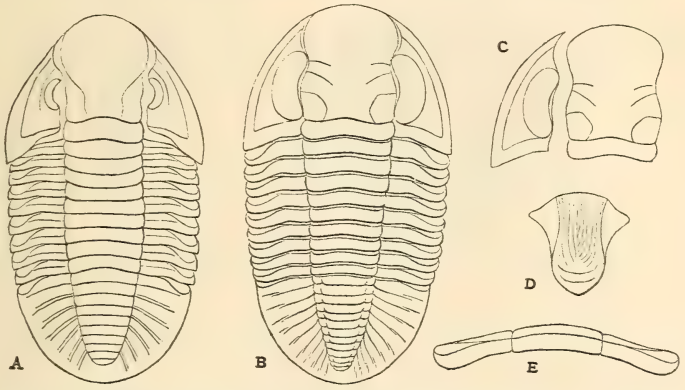

Fig. 405.—A, *Griffithides globiceps*, from the Carboniferous Limestone; B, *Phillipsia Derbiensis*, from the Carboniferous Limestone; C, Glabella and free cheek of the same; D, Hypostome of the same; E, Body-ring of the same. All the figures are enlarged. (After Henry Woodward.)

known to us. In the genus *Phillipsia* (fig. 405, B–E) the body is oval in form, and can be rolled up. The glabella (fig. 405, C) has nearly parallel sides, with two or three lateral furrows, the hindmost of which circumscribe a nearly circular basal lobe on each side. There are only nine body-rings. The tail is semi-oval, distinctly segmented, and with an "entire" margin; and the eyes are large, reticulated, and reniform. *Griffithides* (fig. 405, A) resembles *Phillipsia* in having nine body-rings, but the glabella is pyriform, without lateral furrows, and with the basal lobes inflated, while the eyes are small, lunate, and smooth. *Brachymetopus*, finally, much resembles the preceding in form, but the glabella is small, with lateral furrows but with no basal lobes. The eyes are small and smooth, and no facial sutures are visible. The head-shield is covered with a "small bead-like ornamentation" (Henry Wood-

ward). The thorax is unknown, but the pygidium is large, and the segments of the axis are beaded.

Family 18. Trinucleidæ.—In this singular family (fig. 406) the head-shield is enormously developed, with a wide margin or "limb," which is usually perforated by rounded pores. The glabella is well marked, but eyes are usually wanting, and the facial sutures may be absent. The body-rings are reduced to five or six in number, with grooved pleuræ; and the tail is wide and sub-triangular. The family contains three principal genera, viz., *Trinucleus*, *Dionide*, and *Ampyx*, all of which are Ordovician or Silurian in their range; and its zoological affinities seem to be with the *Harpedidæ*. In the well-known and widely-distributed genus *Trinucleus* (figs. 406, 407) the body is distinctly trilobed; the "limb" of the head-shield is

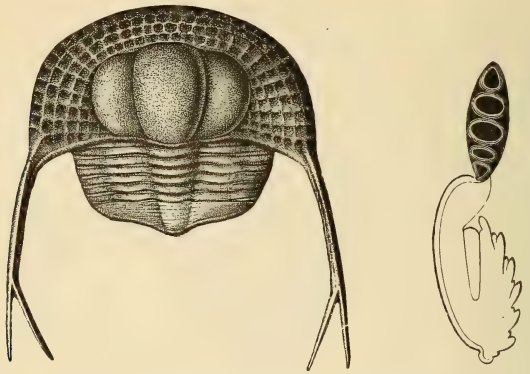

Fig. 406.—*Trinucleus Pongerardi*—Ordovician. The right-hand figure represents a vertical section of a rolled-up specimen.

composed of two lamellæ, and is perforated by numerous larger or smaller foramina; and the "genal angles" are prolonged into conspicuous spines which are usually single, but are forked in *T. Pongerardi*. The glabella is prominent and pyriform, with mere traces of lateral grooves, the facial sutures being rudimentary, and the cheeks being tumid, and generally furnished on each side with a small tubercle seemingly representing the eyes. There are six body-rings; and the tail is triangular, with a distinct axis, and having its margin entire and striated. The genus *Trinucleus* is wholly confined to the Ordovician rocks, and is specially characteristic of the Bala beds. The genus *Dionide* has a sub-quadrangular glabella; and the "limb" of the head-shield, though perforated, is rudimentary, and by absence of the facial sutures becomes continuous with the cheeks. The eyes are wanting, and there are six body-rings. In the curious Ordovician and Silurian genus *Ampyx* (fig. 408) the head is sub-triangular,

with spinose genal angles, and without a perforated "limb." The glabella is prolonged forwards in front of the head-shield as a triangular process, which is often extended into a long spine, while its lateral grooves are obsolete, and eyes are wholly wanting. The facial sutures are present and are discontinuous. There are five or six body-rings, and the tail is sub-triangular. The species of *Ampyx*

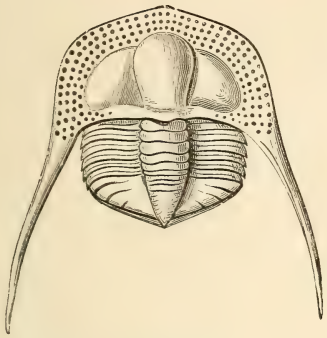

Fig. 407.—*Trinucleus concentricus*. Ordovician. (After Salter.)

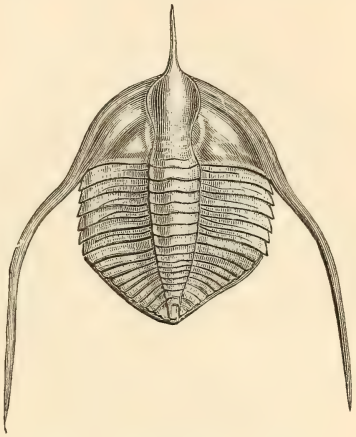

Fig. 408.—*Ampyx nudus*. Ordovician. (After Salter.)

are mostly Ordovician, but a few Silurian forms are known. *Endymionia* (Ordovician) is allied to both *Trinucleus* and *Ampyx*, but wants the perforated border of the former, and the prolonged glabella and genal spines of the latter.

Family 19.—Agnostidæ.—This, the last, family of the Trilobites includes a number of small forms of this order, which range from the Upper Cambrian to near the summit of the Ordovician. The cephalic and caudal shields in this group are nearly equal, and are very similar to one another in form and markings. The thoracic segments are reduced to two only in number, with grooved pleuræ; and both eyes and facial sutures are totally wanting. The type-genus of the family is *Agnostus* itself (fig. 409), which is represented by numerous forms in the Upper Cambrian and Ordovician rocks. *Microdiscus* of the Upper Cambrian (sometimes placed in the *Trinucleidæ* or in the *Olenidæ*) agrees with *Agnostus* in its want of facial sutures and eyes, but it has four body-rings, and the axis of the tail is segmented. Lastly, the *Shumardia* of the Ordovician (Quebec Group) is like *Agnostus*,

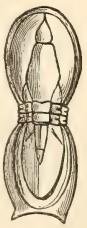

Fig. 409.—*Agnostus princeps*. Upper Cambrian. (After Salter.)

but has both the axis and lateral lobes of the pygidium distinctly segmented.

Division C. Merostomata.

The members of this group are Crustaceans, often of gigantic size, in which the mouth is furnished with mandibles and maxillæ, the terminations of which become walking or swimming feet, and organs of prehension. Two orders are included under the *Merostomata*—viz., the recent King-crabs (*Xiphosura*) and the extinct Eurypterids. By Professor Claus these orders are regarded as forming a special division of Arthropods, with relationships to the *Arachnida*, to which he applies the name of *Gigantostraca*. Professor Ray Lankester has also shown that there are various remarkable features of relationship between *Limulus* and the Scorpions; and the same point has been brought out by Van Beneden from his researches into the development of the King-crabs. Moreover, the investigations of Mr Benjamin Peach would show that there are close and important relationships between the Scorpions and the Palæozoic group of the Eurypterids.

Order I. Xiphosura (Pœcilopoda). — This order includes *Crustacea in which the anterior segments are amalgamated to form a large cephalic buckler, upon the dorsal surface of which are placed the eyes* (when present). *On the under side of the head-shield is placed the mouth, which is furnished with a rudimentary metastoma, and is surrounded by six pairs of appendages, the bases of all but the first pair being modified to act as masticating organs. The segments behind the head-shield may be fused with one another, or may be more or less completely free; and they carry upon their under surface a series of lamellar appendages which are branchial in function. The last segment of the body forms a sword-like movable telson.*

The only existing genus contained in the order *Xiphosura* is *Limulus*, comprising the King-crabs or Horse-shoe Crabs. In this genus (fig. 410) the anterior segments—usually regarded as representing the head and thorax—are fused to form a horse-shoe-shaped cephalothoracic shield. The upper surface of this carries subcentrally a pair of large compound eyes, and also a pair of small larval eyes placed in the middle line in front. On the under side of the head-shield is the mouth, surrounded by six pairs of jointed limbs, the last five pairs having their basal joints spinose, and thus adapted to act as jaws. The first pair of appendages — often regarded as representing the antennæ—are placed in front of the mouth and terminate in nipping-claws. The next four pairs of appendages are also generally chelate, while each of the last pair of legs is terminated by two flat spines, with a whorl of similar spines proximally, being thus adapted for locomotion. Behind

the cephalic buckler comes a second, somewhat rhomboidal shield, the segments of which are immovably welded together, and which is usually regarded as representing the abdomen, though some authorities consider it as the thorax. The lateral margins of this abdominal shield carry movable spines, and on its under surface in front are placed the generative openings, protected by a broad, divided "operculum," which is formed by the first pair of abdominal limbs. The operculum not only covers the reproductive apertures, but more or less extensively conceals the remaining five pairs of abdominal limbs. These latter are much modified, and support a number of delicate lamellæ arranged like the leaves of a book, which act as branchiæ. Lastly, the abdominal shield has movably articulated to its hinder margin a long ensiform "telson" (fig. 410).

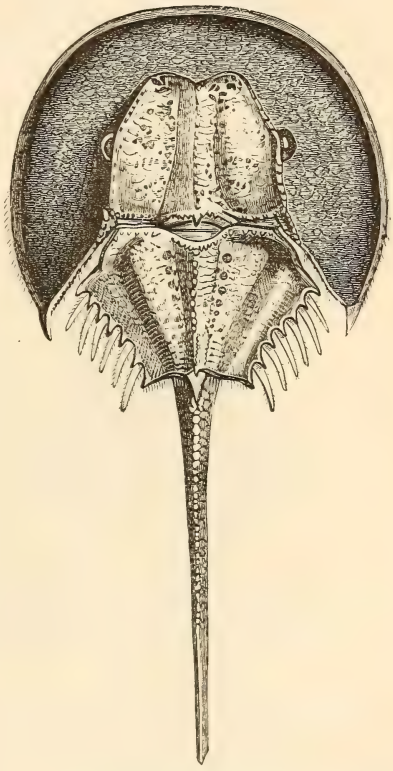

Fig. 410.—*Limulus moluccanus*, viewed from the dorsal aspect, and reduced in size. (Recent.)

The integument of *Limulus* is thoroughly hardened by the deposition of chitine, and forms a resisting shell. Thin sections show that this is largely composed of a peculiar finely tubulated tissue, which has very much the appearance of dentine under the microscope (fig. 411, A). In the inner layer of the shell, the minute tubuli just mentioned are accompanied by a limited number of vertical canals of larger size (fig. 411, A, *c*), the structure thus coming closely to resemble that shown in vertical sections of the shell of the Trilobites.

The embryo of *Limulus* (fig. 382) is destitute of the tail-spine of the adult, this structure only existing in a rudimentary form; and in this stage of its existence, as previously noticed, it bears a strong resemblance to certain of the Trilobites.

It is not necessary here to enter into the vexed question as to

whether *Limulus* should properly be placed among the *Crustacea* or the *Arachnida*. It is sufficient to note that the *Xiphosura* are clearly related to the Eurypterids on the one hand and the Trilobites on the other hand; and that when the natural systematic arrangement of the *Arthropoda* shall have been finally settled, these three orders will necessarily be placed close together. The *Xiphosura* and the *Eurypterida*, in particular, are closely connected together by means of *Hemiaspis* and its allies. So much so is this the case, that while Dr Henry Woodward places *Hemiaspis* and the genera related to it among the Eurypterids, these forms are placed by Zittel among the Xiphosurans, an arrangement which will be followed here.

The existing species of *Limulus* are aquatic in habit and are inhabitants of the sea. The oldest fossil types of the *Xiphosura*

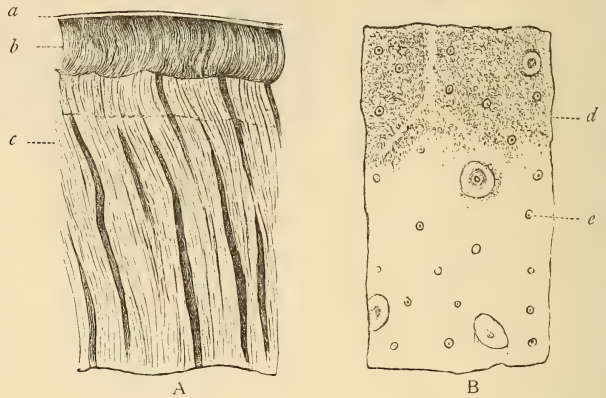

Fig. 411.—A, Part of a transverse section of the tail-spine of *Limulus*: *a*, Outer cuticular layer; *b*, Intermediate finely tubulated layer; *c*, Internal layer of finely tubulated tissue with interspersed larger tubes. B, Part of a tangential section of the inner layer of the cephalic buckler; *d*, Portion of the section showing the minute dots representing the transversely divided tubuli, together with the cut ends of the larger tubes, which are alone shown at *e*. (Original.)

(*Hemiaspis*, *Neolimulus*, &c.), appear in the Silurian rocks. Other ancient types of the order (*Belinurus* and *Prestwichia*) appear in the Carboniferous formation. The oldest types of *Limulus* itself are found in the Triassic rocks.

The *Xiphosura* are divided by Zittel into the two families of the *Hemiaspidæ* and the *Limulidæ*, the former including all the Palæozoic types of the order, while the genus *Limulus* alone is comprised in the latter. In the *Hemiaspidæ*, the cephalic shield is separated from the thorax, and sometimes possesses a "facial suture." The thorax[1] is composed of five or six segments which are usually free

[1] By Packard the head-shield of the *Hemiaspidæ* is regarded as representing the entire cephalothorax; and the free segments which immediately follow this are considered as belonging to the *abdomen* and not to the thorax.

(fig. 412); and the abdomen consists of three or more rings, and is terminated by a spine-like telson. The appendages are as yet unknown.

The genus *Hemiaspis* (fig. 412, A) comprises some singular Silurian Crustaceans, in which there is a semicircular head-shield with a central glabella, and indications of facial sutures and eyes. The thorax is trilobed, and consists of six free segments. There are three free segments in the abdomen, and these are followed by a long spiniform telson. The genus *Pseudoniscus*, also from the Silurian rocks, resembles *Hemiaspis* in many points, and particularly in the possession of free thoracic segments, but there is no distinct line of demarcation between the thorax and the abdomen (fig. 412, B). Another Silurian genus, also closely re-

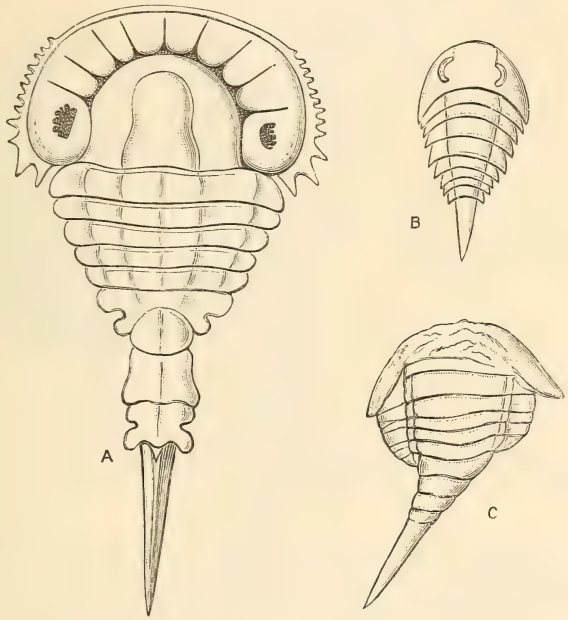

Fig. 412.—A, *Hemiaspis limuloides* (after H. Woodward); B, *Pseudoniscus aculeatus* (after Nieszkowski); C, *Bunodes* (*Exapinurus*) *Schrenkii* (after Nieszkowski). All from the Silurian.

lated to the preceding, is *Bunodes* (*Exapinurus*), in which the thorax likewise consists of free rings, but the last two are fused with one another. There are three movable abdominal rings and a spine-like telson (fig. 412, C), and the animal possessed, like so many of the Trilobites, the power of rolling itself into a ball.

In the remarkable genus described by Dr Henry Woodward from the Silurian rocks of Britain under the name of *Neolimulus* (fig. 413), the head-shield has a general resemblance to that of the recent *Limulus*, and there are traces of a divisional line crossing the head and apparently corresponding with the "facial suture" of the Trilobites. Compound eyes and ocelli seem to be present, and there are six free thoracic segments,

followed, probably, by three free abdominal rings, of which only two have been preserved. A long spiniform telson may be conjecturally added to complete this ancient Limuloid Crustacean. In the Devonian rocks, the only genus of Xiphosurans which has hitherto been recognised with certainty is the *Protolimulus* of Packard, which appears to be nearly related to *Neolimulus*. In the Carboniferous rocks, on the other hand, the Limuloids are represented by a number of forms, the most important genus being *Prestwichia* (fig. 414), which has the general form of *Neolimulus*, but in which the thoracic and abdominal segments are not marked off from one another, and are all anchylosed. The genus *Euproöps*, from the Coal-measures of North America, is hardly separable from the preceding, but the eyes are situated on the anterior edge of the

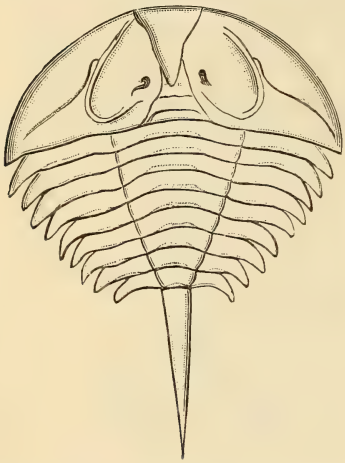

Fig. 413.—*Neolimulus falcatus*, enlarged about three times. Silurian. (After Henry Woodward.)

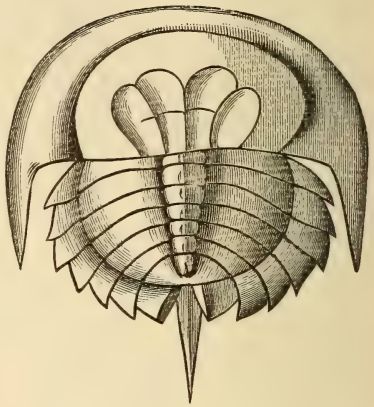

Fig. 414.—*Prestwichia rotundata*. Coal-measures.

cephalic buckler. Another well-known Carboniferous genus is *Belinurus*, which agrees with the preceding in having five thoracic and three abdominal segments, together with a long tail-spine, but in which the thoracic rings are free and movable, while those of the abdomen are anchylosed with one another. It would also seem probable that the singular Crustacean fossils which have been described from the Coal-measures under the name of *Cyclus*, are really, as maintained by Dr Henry Woodward, the young forms of such Carboniferous Xiphosurans as *Belinurus* and *Prestwichia*. The very similar Triassic fossils, for which the generic name of *Halycine* has been proposed, are probably also the larval forms of Limuloid Crustaceans.

The family of the *Limulidæ* is distinguished from that of the *Hemiaspidæ* by the fact that the cephalic and thoracic segments are amalgamated to form a cephalothoracic shield, the upper surface of which bears two compound eyes and a pair of simple eyes. The abdominal segments are amalgamated with one another to form a

second post-cephalic shield, which is terminated by the movable, spine-like telson. The only genus of this family is *Limulus* itself, the characters of which have been already treated of in some detail. The earliest undoubted fossil species of *Limulus* appear in the Trias of Europe, and other representatives of the genus are found in the Jurassic rocks (the Lithographic Slates of Germany), and in the

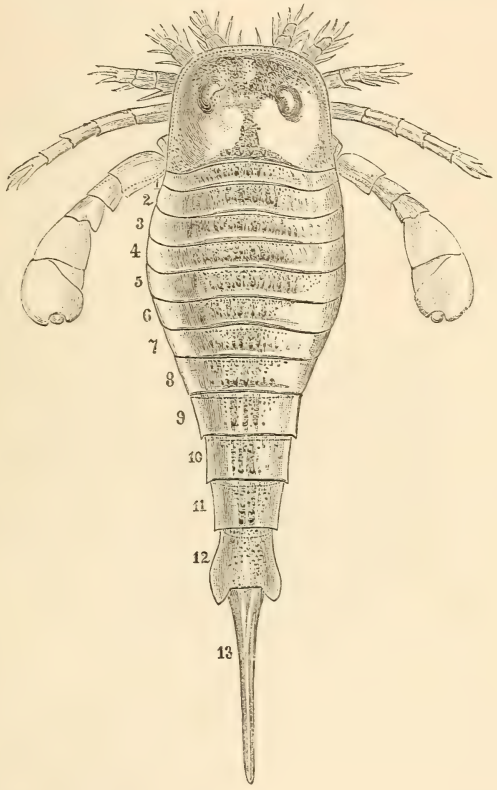

Fig. 415.—*Eurypterus Fischeri*, from the Silurian rocks of Oesel, viewed from above and restored, the size being about one-fifth of nature. The segments behind the carapace are numbered, the first six being sometimes considered as thoracic. (After Friedrich Schmidt. Copied from Zittel.)

Cretaceous and Tertiary deposits. Of the existing species of the genus, one is found on the east coast of North America, and others occur on the eastern shores of Asia and in the Malayan Archipelago.

Order II. Eurypterida.—The Eurypterids are *large Crustaceans* (fig. 415), *in which the body is elongated and compressed, and the chitinous integument is ornamented with a characteristic scale-like*

sculpturing. The anterior part of the body is covered with a carapace, which carries a pair of large, marginal, or subcentral eyes, and a pair of small ocelli placed near the centre. On the under side of the carapace is the opening of the mouth, furnished behind with a large undivided metastoma and with a series of jointed appendages (five or six pairs in number), of which the first are præoral, and represent antennæ, while the remainder are modified for mastication or locomotion, the last pair forming usually great swimming-feet. Behind the carapace the body consists of numerous free thoracico-abdominal segments, certain of the anterior of which are furnished below with divided lamellæ, which concealed the branchiæ. The hinder segments carry no appendages, and the abdomen terminates in a spine-like or paddle-shaped telson.

The integument of the Eurypterids is hardened by chitine, and when transparent fragments are examined under the microscope, these exhibit a reticulated structure, numerous clear rounded corpuscles, of various sizes, appearing to be disseminated in a horny matrix; the crust thus assuming a punctated or porous aspect. The characteristic "scale-marking" is the result of the development at intervals of curved linear thickenings of the exoskeleton.

The anterior part of the body in the Eurypterids is covered by a comparatively short, semicircular, or subquadrate carapace, which is considered by Woodward, Schmidt, and Zittel as representing the head only, but which is regarded by Claus and Hall as a cephalothorax. The upper surface of the carapace carries a pair of large, prominent, faceted, compound eyes, which may be subcentral, or may be placed on the margin of the head-shield. There is also a pair of small ocelli, usually placed close together, subcentrally.

On the under side of the carapace is the opening of the mouth, surrounded by a series of jointed appendages. The first pair of appendages (fig. 416, *an*) are præoral in position, and represent the antennæ. They terminate in pincers in *Pterygotus* (fig. 416, *an*), but are stated by Fr. Schmidt to have the form of very slender jointed organs in *Eurypterus*. The remaining appendages are similar to those of *Limulus* in having their bases spinous, and in officiating as jaws. Woodward recognises four pairs of these; but according to Fr. Schmidt there are five pairs, the total number of appendages on the under side of the head-shield being thus six pairs. The anterior appendages behind the antennæ may represent mandibles and maxillæ, and they have the form of slender jointed organs, with dilated and serrated basal joints (fig. 416, *gn*). The last pair of appendages, regarded by Woodward as maxillipedes (fig. 416, *mx*), are of great size, and while their bases are dentated to fit them for mastication, they are usually dilated distally so as to form powerful swimming-paddles. The mouth is a longitudinal

fissure on the under side of the head, surrounded by the toothed bases of the limbs, and provided behind with a large undivided metastoma (fig. 416, *m*), while in some cases a hypostome or upper lip appears to be present as well.

Behind the carapace the body consists of thirteen free segments, counting the telson as one. By Claus and Hall the whole of these segments are regarded as belonging to the abdomen. By other

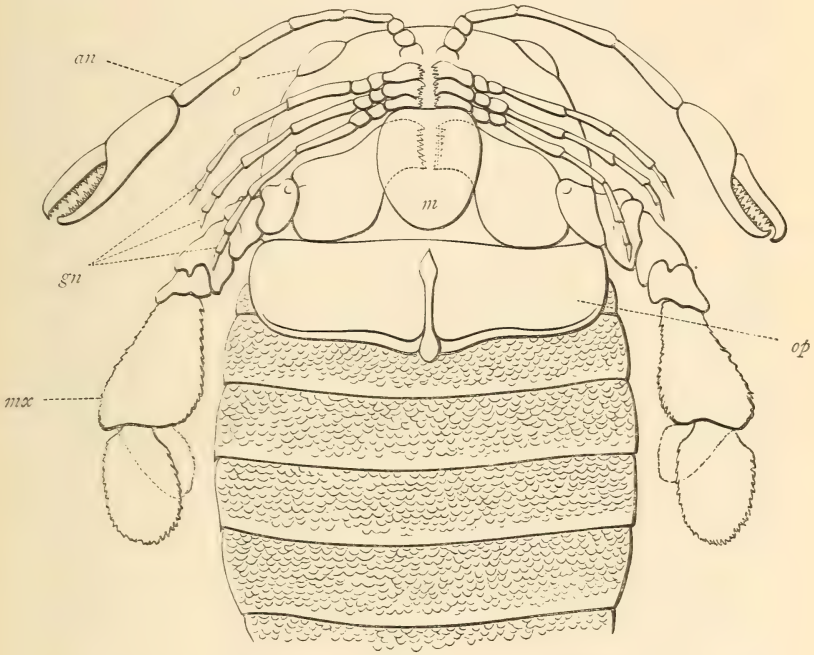

Fig. 416.—Under side of the head and the following segments of *Pterygotus Anglicus*, restored. *o*, The large compound marginal eyes; *an*, The first pair of appendages, chelate, and representing antennæ; *gn*, Three pairs of slender "gnathopods," with spinose bases, placed on the sides of the mouth-opening (according to Fr. Schmidt, there are *four* pairs of these organs); *mx*, the last pair of appendages ("maxillipedes"), developed into great swimming-feet, but acting by their bases as jaws; *m*, Metastoma, drawn as if it were transparent, so as to show the toothed bases of the last pair of appendages below it; *op*, Operculum. The "scale-marking" is only represented on the segments behind the operculum. (After Henry Woodward.)

authorities, however—as, for example, by Fr. Schmidt—the anterior six of these segments are regarded as belonging to the thorax, while the posterior seven are looked upon as forming the abdomen. Immediately behind the carapace, on the inferior aspect of the body, is a broad lamellar plate, which is divided into two lateral halves by a narrow median process (fig. 416, *op*), and which is known as the "operculum." This plate, like the structure which bears the same name in the King-crabs, doubtless protected the openings of the

reproductive organs, and also served to conceal the leaf-like gills, fragments of which are sometimes found in the fossil state. According to Fr. Schmidt, the segments immediately following the "operculum" have their ventral side formed, each, by a pair of lamellar plates, which meet in the middle line, and which are regarded by this observer as modified thoracic appendages carrying branchiæ. According to the investigations of Mr Benjamin Peach, some Eurypterids were further provided with well-developed pectinated organs, apparently similar in form and structure to the so-called "combs" (*pectines*) of the existing Scorpions. Lastly, the seven hindmost segments of the body are undoubtedly devoid of appendages of any kind, and the last of these is the "telson." The form of this varies, being lanceolate or bilobate in *Pterygotus* and *Slimonia*, but narrow and sword-shaped in *Eurypterus* and *Stylonurus*.

There are at present no materials available for working out the development of the Eurypterids, but there is every reason to suppose that the berry-like bodies which are found in the Old Red Sandstone of Scotland, and which have been described under the name of *Parka decipiens*, are really the eggs of Crustaceans belonging to this order.

There can be no question as to the importance of the relationships between the Eurypterids and the Scorpions; and many high authorities consider that the order *Eurypterida* should be removed from the *Crustacea* and placed in the series of the *Arachnida*. There is, however, no reason for doubting that the Eurypterids were water-breathing animals, provided with branchiæ; and as the nature of the respiratory organs constitutes, perhaps, the most weighty of the distinctions between the closely related classes of the *Crustacea* and the *Arachnida*, it would seem proper to regard the *Eurypterida* as an ancient type of the *Crustacea*, in which are preserved certain of the characters which must have been possessed by the ancestral Arthropods from which these two classes originally diverged.

The nature of the deposits in which the remains of Eurypterids are found, and of the fossils associated with them, would prove that these animals were essentially marine, their habits, probably, being very similar to those of the existing King-crabs. It is, however, possible that certain of the Eurypterids were inhabitants of brackish, or even of purely fresh, waters. As regards their geological range, the Eurypterids seem to have appeared for the first time in the Ordovician rocks, but comparatively little is known of the early representatives of the order. On the other hand, Eurypterids abound in the Silurian rocks, and it is in this system of deposits that the order seems to have attained its maximum development. Numerous Devonian Eurypterids are also known, and the genus *Eurypterus* is represented in the Carboniferous rocks, while a doubtful repre-

sentative of the order (*Campylocephalus*) has been recorded from the Permian rocks of Russia. With the close of the Palæozoic period, however, the order appears to have undergone complete extinction.

The four most important genera of the Eurypterids are *Eurypterus*, *Pterygotus*, *Slimonia*, and *Stylonurus*. In *Eurypterus* (fig. 415) there are five pairs of legs attached to the under surface of the head-shield, all of which have their bases modified to act as masticatory organs, and the last pair of which are developed into powerful swimming-paddles. There is also, according to Fr. Schmidt, an additional, præoral pair of appendages, in the form of delicate jointed filaments, which represent the antennæ but are not chelate. Most of the species of *Eurypterus* are found in the highest deposits of the Silurian rocks ; but there are a few Devonian species, and the Carboniferous rocks have likewise yielded representatives of the genus (*e.g.*, the *E. Scouleri* of the Scotch Carboniferous rocks).

The genus *Pterygotus* (fig. 416) is principally Silurian and Devonian, the largest species (*Pterygotus Anglicus*)—sometimes attaining a length of nearly six feet—being found in the Old Red Sandstone of Scotland ; but Barrande has described forms of the genus from the Ordovician rocks of Bohemia. *Pterygotus* differs from *Eurypterus*, among other characters, in the marginal position of the large compound eyes, and in the fact that the præoral appendages (antennæ) are very long and terminate in nipping-claws. The telson of *Pterygotus*, further, is broad and lanceolate, whereas that of *Eurypterus* is long and pointed. The Silurian genus *Slimonia* resembles *Pterygotus* in the form of the telson and in the marginal position of the compound eyes, but differs from it in the quadrate form of the head-shield and in the structure of the limbs. Finally, the Silurian and Devonian genus *Stylonurus* resembles *Eurypterus* in the possession of an ensiform telson, and in its general structure ; but the last two pairs of limbs are developed into long slender rowing-organs, which reach nearly to the hinder extremity of the body.

CHAPTER XXX.

CRUSTACEA—continued.

Sub-class III.—Malacostraca.

The Crustaceans included in the sub-class *Malacostraca* (*Thoracipoda*, Woodward) are distinguished by the possession of a generally *definite* number of body-segments; seven somites going to make up the thorax, and an equal number entering into the composition of the abdomen (counting, that is, the telson as a somite). The *Malacostraca* are divided into two primary divisions, termed respectively the *Hedriophthalmata* and the *Podophthalmata*, according as the eyes are sessile or are supported upon eye-stalks.

Division A. Hedriophthalmata.

This division comprises those *Malacostraca* in which the eyes are sessile, and the body is mostly not protected by a carapace. It comprises the two orders of the *Isopoda* and *Amphipoda*. The eyes are generally compound, but sometimes simple, and are placed on the sides of the head. The head is almost always distinct from the thorax, and the mandibles are often furnished with a palp. Typically there are seven pairs of feet in the adult, hence this division has been called *Tetradecapoda* by Agassiz.

Order I. Amphipoda.—The members of this order are Crustaceans, mostly of small size, in which *the body is laterally compressed, and the thorax consists of seven segments, carrying seven pairs of legs. The abdomen is mostly well developed, and consists of seven segments. The gills are lamellar or vesicular, and are attached to the basal joints of the thoracic legs. The seven pairs of thoracic limbs are directed partly forwards and partly backwards.* It is from this latter circumstance that the name of the order is derived.

The order of the Amphipods comprises both marine and fresh-water forms, many familiar types, such as the Sand-hoppers (*Talit-*

rus) and Shore-hoppers (*Orchestia*), being more or less amphibious in habit, while some genera (such as *Gammarus*) possess both marine and fresh-water representatives. The geological history of the Amphipods is still very imperfectly known. If the incompletely understood Palæozoic genera *Gampsonyx*, *Palæocaris*, *Palæorchestia*,

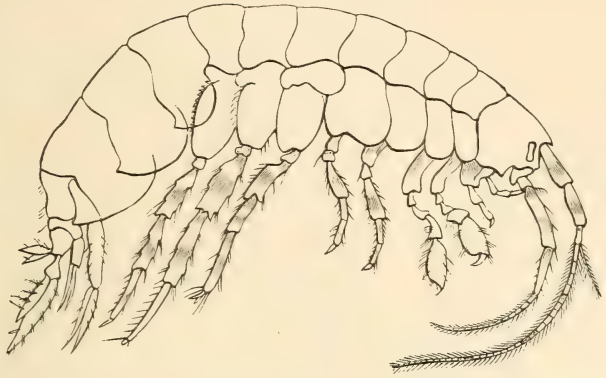

Fig. 417.—*Gammarus locusta*, enlarged about four times. Recent. (After Spence Bate and Westwood).

and the forms allied to these, be excluded from the order, the number of known fossil forms of the order is very small. If the genus *Necrogammarus* described by Dr Henry Woodward from the Silurian rocks of Britain, be truly referable here, it is the oldest type of the Amphipods at present known. Hardly less certain is the position of the Permian genus *Prosoponiscus* (*Palæocrangon*),

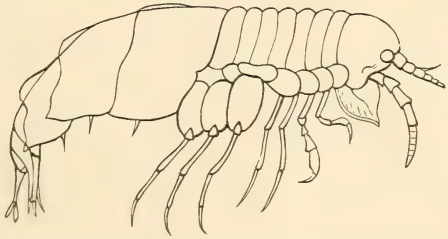

Fig. 418.—*Prosoponiscus* (*Palæocrangon*) *problematicus*, viewed from one side, and partially restored. From the Magnesian Limestone (Permian) of Durham. (After Spence Bate.)

which Mr Spence Bate has described as related to the living *Phædra antiqua*. The fossil forms of the *Amphipoda* from the Tertiary series are almost exclusively from fresh-water deposits, and either belong to such existing genera as *Gammarus* or are nearly allied to other living types. No fossil representatives of the little group

of parasitic Amphipods included under the name of *Læmodipoda* have been as yet discovered.

Order II. Isopoda.—In this order *the head is always distinct from the segment bearing the first pair of feet. The respiratory organs are not thoracic*, as in the preceding order, *but are attached to the inferior surface of the abdomen, and consist of leaf-like branchiæ, which in the terrestrial species are protected by plates which fold over them. The thorax is composed of seven segments, bearing typically seven pairs of limbs*, which, in the females, have marginal plates, attached to their bases, and serving to protect the ova. The num-

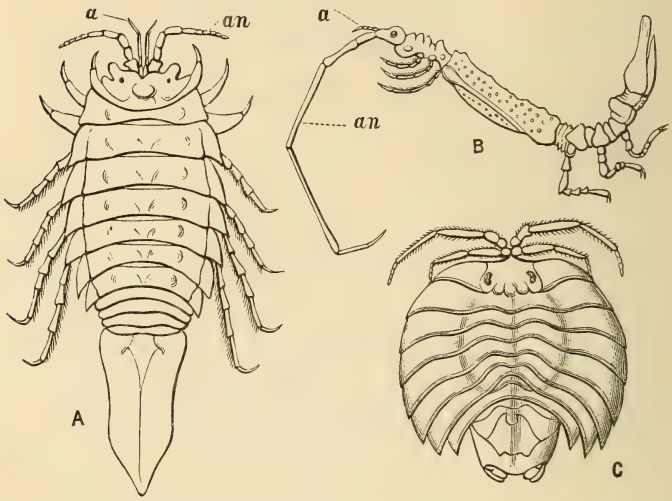

Fig. 419.—Recent Isopoda. A, *Idotea entomon*, enlarged; B, *Arcturus longicornis*, enlarged; C, *Serolis Scythei*: *an*, Antennæ; *a*, Antennules. (After Gerstaecker, Spence Bate and Westwood, and Lütken.)

ber of segments in the abdomen varies, but is never more than seven. The abdominal segments are in many Isopods coalescent, and form a broad caudal shield, beneath which the branchiæ are carried (fig. 419, A).

The recent Isopods are for the most part of small size, and are of the most varied habit. Many forms are strictly marine, some forms occurring even at great depths (over 2000 fathoms), but very many types are either inhabitants of shallow water or live between tide-marks. Some forms, such as the *Bopyridæ*, are parasitic in the adult condition. Many Isopods live in fresh waters, some of these belonging to genera which are also represented by marine forms. Other Isopods, like the Wood-lice (*Oniscidæ*) are terrestrial in habit.

As in the case of the Amphipods, the geological history of the Isopods is very imperfectly known. The Palæozoic Arthropods which have been referred here, such as the problematical *Arthropleura* of the Carboniferous rocks, and the form described by Dr Henry Woodward from the Old Red Sandstone under the name of *Prœarcturus*, are of doubtful affinities. The earliest unquestionable Isopods are found in the Jurassic rocks (the Lithographic Slates of Germany), in which the order is represented by the extinct genera *Urda* and *Ægites*. In the Upper Jurassic (Purbeck beds) of Britain is found the *Archæoniscus Brodiei* (fig. 420), often in considerable numbers, the genus being apparently referable to the recent family of the *Ægidæ*. To the same family belongs the extinct genus *Palæga*, species of which are found in the Cretaceous and Tertiary rocks. A tolerably abundant Tertiary genus is *Eosphæroma*, which belongs to the recent family of the *Sphæromidæ*. Lastly, the terrestrial family of the Wood-lice (*Oniscidæ*) is represented in late Tertiary deposits by such existing genera as *Armadillo*, *Porcellio*, and *Oniscus* itself.

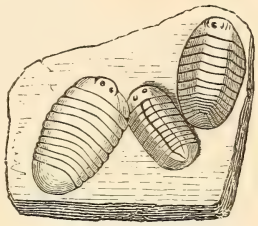

Fig. 420.—*Archæoniscus Brodiei*, a fossil Isopod from the Purbeck Beds.

Division B. Thoracostraca or Podophthalmata.

The Crustaceans included in this division possess compound eyes which are usually placed upon movable peduncles; while the anterior part of the body is covered with a "carapace" or shield, which covers the head and the anterior thoracic segments at any rate, and often protects the entire cephalothorax. The body consists of nineteen undoubted segments, of which thirteen belong to the cephalothorax and six to the abdomen. If the ocular ring and the telson be counted as segments, there are then twenty-one segments altogether. All of the *Thoracostraca* except certain of the Shrimps (*Penœidæ*) pass through "Zoea" stages in their development. The division *Thoracostraca* comprises the four orders of the *Cumacea*, the *Schizopoda*, the *Stomatopoda*, and the *Decapoda*, of which the last includes the most highly organised and familiar examples of the class *Crustacea*. Of these orders, the first two have no direct fossil representatives, though we may consider in connection with the Schizopods certain Palæozoic Crustaceans, which are possibly ancestral types of the order. The Stomatopods are represented by few fossil forms, beginning, perhaps, in the Carboniferous rocks. On the other hand, there are numerous known fossil forms of the

Decapod Crustaceans, especially in the Mesozoic and Tertiary deposits; but the palæontological interest of these is comparatively small, and it will be sufficient here to give a brief sketch of the general geological history of the three great tribes into which the order *Decapoda* is divided.

Order I. Cumacea.—This order includes small marine Crustaceans, in which there is *a short carapace covering the head and the anterior thoracic segments. The eyes are sessile, and the mouth-organs resemble those of the Isopoda. The two anterior pairs of legs at least possess natatory exopodites, and the branchiæ are attached to the epipodites of the maxillipedes. The abdomen is elongated and composed of six segments, and a telson may be present or absent.*

The *Cumacea* are regarded by G. O. Sars as an order of *Crustacea* related on the one hand to the Schizopods or Macrurous Decapods, and on the other hand to the *Isopoda*. No fossil forms of the order are known.

Order II. Schizopoda.—This order includes the "Opossum Shrimps" (*Mysis*) and their allies, comprising small Crustaceans which are in many respects related to the *Decapoda*. According to G. O. Sars, the Schizopods occupy "the most primitive position

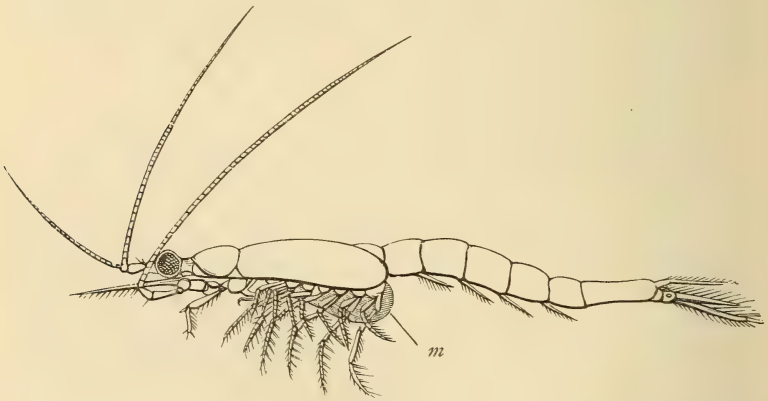

Fig. 421.—"Opossum Shrimp" (*Mysis oculata*). *m*, Marsupial pouch. (After G. O. Sars.)

within the division *Podophthalmia*, being apparently the least modified forms, in which the original characters distinguishing the progenitors of the whole division would seem to exhibit least change." The correctness of this view is shown by the fact that many of the Podophthalmate Crustaceans pass in their development through a "Mysis-stage," in which they present marked Schizopodous characters. The Schizopods are characterised by the fact that *the*

thoracic limbs are eight on each side, and are provided each with an exopodite and endopodite (fig. 421), *the exopodites being natatory in function. A cephalothoracic shield is present, and there is usually only a single pair of maxillipedes. The gills are attached to the thoracic legs, or, exceptionally, to the abdominal feet. The ova are carried beneath the thorax of the female, usually in a marsupial pouch formed by leaf-like plates produced from the bases of the legs* (fig. 421, *m*). *The telson often possesses minute terminal appendages or spines.*

The Schizopods are distinguished from the Decapods by the larger number of the thoracic limbs, and by the fact that these appendages have well-developed exopodites, as well as by the fact that the gills are not carried in branchial chambers formed by a downward prolongation of the sides of the carapace. In *Mysis* and its allies true branchiæ are wanting. With the single exception of the *Mysis relicta* of the great lakes of Sweden and North America, all the Schizopods are inhabitants of the sea, extending their range to considerable depths.

No undoubted fossil forms of the *Schizopoda* are as yet known, but a brief consideration may be given here to the singular Palæozoic genera *Palæocaris* and *Gampsonyx*, which some authorities regard as aberrant members of the *Amphipoda*, but which are considered by Packard as being probably ancestral types of the Schizopods. The genus *Palæocaris* (fig. 422) includes peculiar elongated Crustaceans from the Coal-measures of North America and Britain, in which there is a short cephalothoracic shield, but the hinder thoracic segments are free. There are two pairs of antennæ, of nearly equal length, and the limbs do not appear to be bifid. The telson has a pair of "stylets" on each side, and the condition of the eyes has not been clearly ascertained. The genus *Acanthotelson*, also from the Coal-measures, appears to be related to *Palæocaris*, as, possibly, are the genera *Palæorchestia* (Carboniferous) and *Nectotelson* (Permian), but the true relationships of these forms are very uncertain. Another Carboniferous genus which may perhaps find a place here is *Gampsonyx*, including small Crustaceans which have a general resemblance to the Amphipods in appearance, but in which the limbs seem to have been of the Schizopodous type.

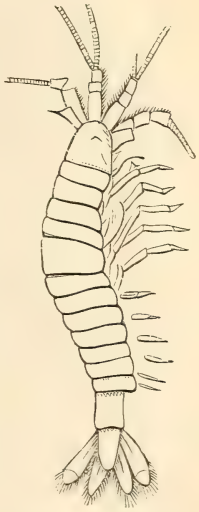

Fig. 422. — *Palæocaris typus*, slightly enlarged. From the Coal-measures of North America. (After Meek and Worthen.)

Order III. Stomatopoda.—This order includes the recent

Locust-shrimps (*Squilla*), all of which are inhabitants of the sea. The Crustaceans of this order (fig. 423) have *a short cephalothoracic carapace, which does not protect the hinder segments of the thorax. There are five pairs of maxillipedes, and three pairs of thoracic legs. The branchiæ are not enclosed in a cephalothoracic gill-chamber on each side, but are in the form of tufts attached to the abdominal feet. The eyes and antennæ are attached to a somite which is not soldered to the cephalothorax.*

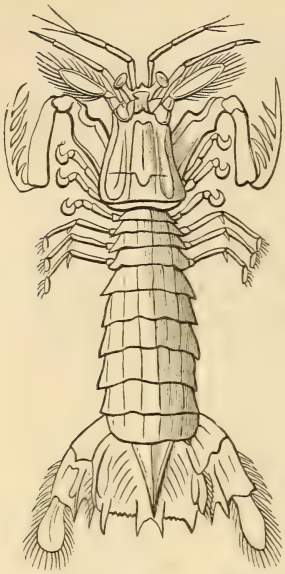

Fig. 423.—*Squilla mantis*, the Locust-shrimp.

As regards their distribution in time, it is doubtful if any Palæozoic types of the Crustacea can be referred to this order, but the genera *Necroscilla* and *Diplostylus*, of the Coal-measures, may possibly be ancient representatives of the *Stomatopoda*. In the Jurassic rocks (Lithographic Slates) of Germany is found the genus *Sculda*, which is related to the recent genus *Squilla*, and species of the latter have been described from the Cretaceous rocks, while others occur in the Eocene Tertiary.

Order IV. Decapoda.—This order includes the Shrimps and Lobsters, the Hermit-crabs, and the true Crabs, and comprises the most highly organised of all the *Crustacea*. Most of the Decapods are aquatic in their habits, and they are usually protected by strong resisting shells. There is always a complicated set of "gnathites," or appendages modified for masticatory purposes, surrounding the mouth. *The ambulatory feet are made up of five pairs of legs* (hence the name of the order); *the first pair—and often some other pairs behind this—being "chelate," or having their extremities developed into nipping-claws. The branchiæ are pyramidal, and are contained in cavities at the side of the thorax. The carapace is well developed, and covers all the segments of the head and thorax.*

The *Decapoda* are divided into three tribes, termed respectively the *Macrura*, *Anomura*, and *Brachyura*, and characterised by the nature of the abdomen.

Tribe A. Macrura. — This tribe includes the "Long-tailed Decapods," such as the Lobsters, Cray-fish, Shrimps, and Prawns, in which the abdomen is well developed, often longer than the

cephalothorax, and its posterior extremity is in the form of a powerful natatory organ or caudal fin. The recent Macrurans are mostly marine in habit, but some typical forms (the Cray-fishes) are inhabitants of fresh water. The earliest fossil representatives of the *Macrura* are certain Shrimp-like Crustaceans which appear in the Devonian and Carboniferous rocks, but the group undergoes a great development in the Mesozoic period, and many Tertiary forms are known as well. It will be sufficient here to give a general sketch of the geological history of the group, without discussing its different families in any detailed manner.

The oldest known Macruran is the Shrimp-like *Palæopalæmon* of the Devonian rocks of North America, the general characters of which would justify its reference to the existing family of the Shrimps and Prawns (*Caridida*). To the same family may be referred the Carboniferous genera *Anthrapalæmon* (fig. 425), *Crangopsis*, and *Pygocephalus*. In *Anthrapalæmon*, there is a well-developed carapace, which is furnished with a beak or "rostrum," and possesses serrated lateral margins. There are five pairs of thoracic legs; the abdomen is composed of free segments, and there is a caudal fin, formed by the telson along with the last pair of swimmerets. No undoubted representatives of the *Macrura* have hitherto been detected in the Permian rocks, but the Trias has yielded a number of Long-tailed Decapods belonging to the families of the Shrimps (*Penæus* and *Æger*), the *Eryonidæ*, and the *Glyphæidæ* (*Pemphix*, *Lithogaster*, &c.) It is, however, in the Jurassic rocks that the *Macrura* attain their maximum development as fossils, all the recent families of the order having now come into existence, and some of them attaining here their culminating point. The Shrimps (*Caridida*) are represented by genera

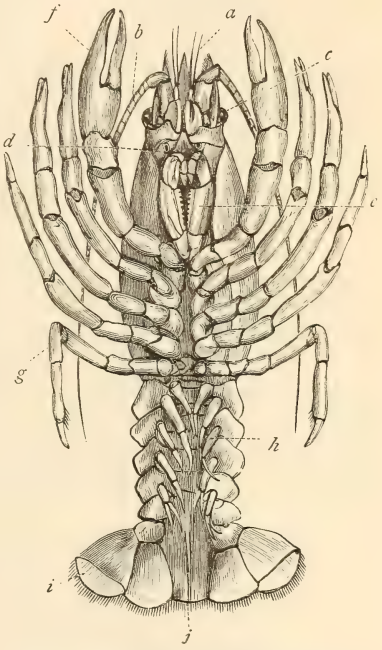

Fig. 424.—The common Cray-fish (*Astacus fluviatilis*), viewed from below. *a*, Antennules; *b*, Antennæ; *c*, Eyes; *d*, Opening of antennary gland; *e*, Last pair of foot-jaws; *f*, One of the great chelæ; *g*, Fifth thoracic limb; *h*, Swimmerets; *i*, The last pair of swimmerets; *j*, The opening of the anus below the telson.

such as *Penæus* and *Æger;* the Spiny Lobsters (*Palinuridæ*) are exemplified by the singular *Mecochirus* (fig. 426) of the Solenhofen Slates, in which the first pair of ambulatory limbs are enormously elongated, but do not terminate in pincers; the *Glyphæidæ* are represented by *Glyphæa* itself, and the genus *Pseudastacus* takes the place of the modern Lobsters. The most remarkable group of the Jurassic *Macrura* is, however, that of the *Eryonidæ*, of which the principal genus is *Eryon* itself. This interesting family has representatives in the Trias, and is very widely distributed in the Jurassic and Cretaceous rocks, while recent investigations have shown that a few forms of the group (such as *Willemoësia*) still maintain their existence at the bottom of the deep sea. In *Eryon* (fig. 427), the carapace is large and broad, and nearly quadrate in figure, whilst the antennæ are very small; the first four pairs of ambulatory legs are chelate, and the first pair are much longer than the others; and the caudal extremity is constituted by the triangular telson and the dilated last pair of swimmerets. Beautifully preserved examples of *Eryon* are found in the Lithographic

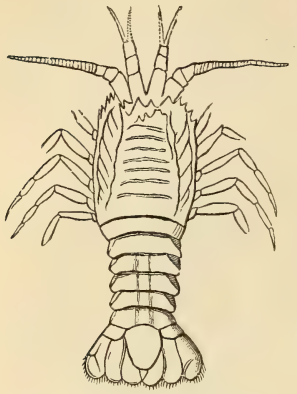

Fig. 425.—*Anthrapalæmon gracilis*, of the natural size. From the Coal-measures of North America. (After Meek and Worthen.)

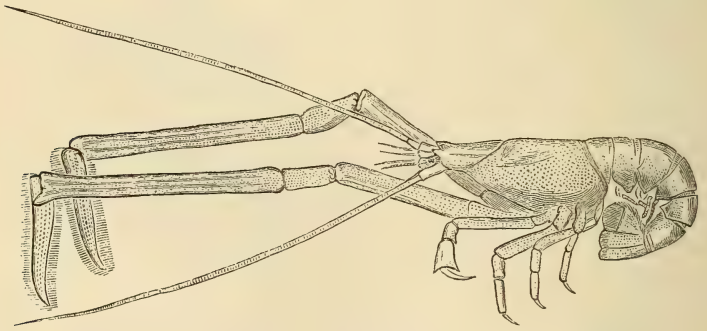

Fig. 426.—*Mecochirus longimanus*, from the Lithographic Slates of Eichstadt, one-half the natural size. (After Zittel.)

Slates of Germany, and in the same deposits are found the remains of "Phyllosomæ," which are to be regarded as the larval stages of the former. In the Cretaceous rocks, Macrurous Decapods are tolerably numerous, and belong to all the principal sections of the

tribe. Among the more characteristic Cretaceous genera may be mentioned *Enoploclytia*, *Hoploparia*, *Meyeria*, *Palinurus*, and *Scyllarus*. Very abundant also in parts of the Cretaceous series are the great chelæ of burrowing Crabs belonging to the genus *Callianassa*, a type which appeared in the Jurassic rocks, and which survives at the present day. In the Tertiary rocks, finally, the remains of *Macrura* are comparatively scanty, and present few points of special interest. The recent genus *Homarus*, including the common Lobster, appears in the Oligocene deposits, and in the fresh-water Tertiary deposits of North America are found the remains of Cray-fishes (*Astacus*) essentially similar to existing forms.

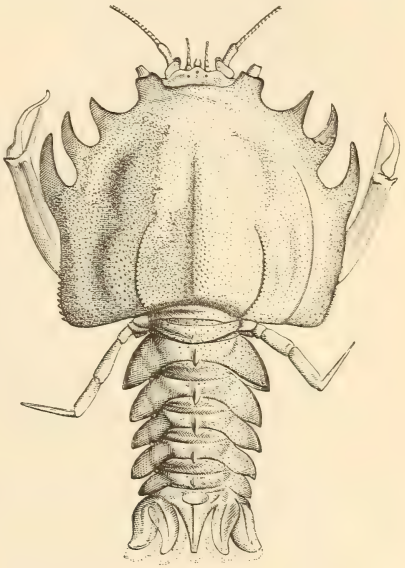

Fig. 427.—*Eryon arctiformis*. Jurassic rocks. (Solenhofen Slates.)

Tribe B. Anomura.—The Decapods which belong to this tribe are distinguished by the condition of the abdomen, which is neither so well developed as in the *Macrura*, nor so rudimentary as in Crabs. The last pair of thoracic limbs are reduced in size. Further, the abdomen does not terminate posteriorly in a caudal fin, as in the *Macrura*.

The division *Anomura* must be regarded as an artificial assemblage, composed of modified forms of both the *Macrura* and *Brachyura*. It is, in fact, impossible to draw a rigid line between the *Anomura* and the *Brachyura*—the two tribes being connected by transitional forms, which might with equal propriety be placed in either. The most characteristic forms of the *Anomura* are the "Hermit-crabs" (*Pagurus*, *Cœnobita*, &c.), and the "Plated Lobsters" (*Galathea*). The Hermit-crabs are interesting on account of their habit of protecting the soft abdomen within the empty shell of some Mollusc (fig. 428). Many of the Hermits, such as the *Cœnobitæ* of the tropics, are terrestrial in their habits, and commonly employ the shells of snails for their borrowed dwelling. As the *Cœnobitæ* migrate to the sea for the purpose of pro-

ducing their eggs, it is conceivable that by their agency a curious and puzzling intermixture of land-shells with marine types of Molluscs might be effected.

With regard to the distribution of the *Anomura* in time, our knowledge is at present very imperfect. If the group of Decapods represented by the living Sponge-crabs (*Dromia*) be referred to the *Brachyura*, then it is doubtful if any remains of the *Anomura* have been found in any Mesozoic deposit, while Palæozoic forms are

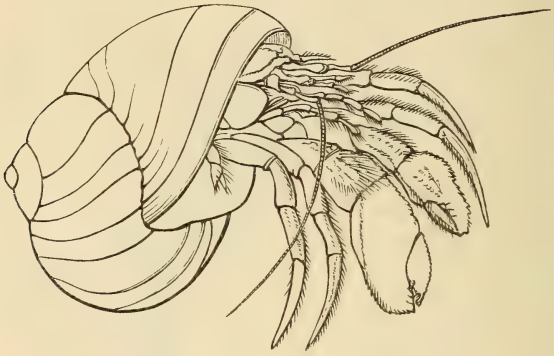

Fig. 428.—Hermit-crab (*Cœnobita*) in its borrowed shell. After Morse.

wholly unknown. The claws of a form resembling *Galathea* have been recorded as occurring in the Faxoe Chalk; but with this exception the earliest unquestionable remains of Anomurous Decapods are referable to the genus *Pagurus*, and are found in the Eocene deposits.

Tribe C. Brachyura.—The "short-tailed" Decapods, or Crabs, are distinguished from the two preceding tribes by the rudimentary condition of the abdomen, which is very short, and is tucked up beneath the cephalothorax, the latter being disproportionately large. There is no caudal fin, and there are from one or two (males) to four (females) pairs of abdominal appendages, which are employed by the females in carrying the ova. The Crabs are mostly furnished with ambulatory limbs, and are rarely formed for swimming, most of them being littoral in their habits, and some even living inland.

With regard to their geological history, it is very doubtful if any genuine representatives of the *Brachyura* have been hitherto detected in the Palæozoic series. The *Gitocrangon granulatus* of the Devonian rocks, the *Brachypyge carbonis* of the Carboniferous, and the *Hemitrochiscus paradoxus* of the Permian deposits, which have been supposed to be ancient types of the *Brachyura*, are all more or less problematical in nature. Even in the Jurassic rocks the

evidence of the existence of genuine Crabs is not perfectly clear; since the *Palœinachus longipes* of the Forest Marble (Lower Oolites), described by Dr Henry Woodward as a Crab, is not completely known, and the Jurassic genus *Prosopon* may perhaps be referable to the *Anomura*. In the Cretaceous rocks there are various Decapods of the family of the Sponge-crabs, which form a transitional group between the *Brachyura* and *Anomura*, such as the genus *Dromiopsis;* but there are also genuine Crabs, such as *Palæocorystes*, *Eucorystes*, *Necrocarcinus*, *Etyus*, and *Xantho*, representing several of the existing families of the *Brachyura*. The Eocene deposits, and particularly those of Britain (the London Clay), have proved very rich in the remains of Brachyurous Decapods, some of the forms of this period belonging to extinct genera (such as *Micromaia*, *Psammocarcinus*, *Palæocarpilius*, fig. 429, *Lobocarcinus*, *Xanthilites*, and, above all, *Xanthopsis*), while others are referable to such existing genera as *Cancer* and *Xantho*. The later Tertiary deposits have yielded comparatively few remains of *Brachyura*, and these of little special interest, but the fresh-water genus *Telphusa* and the terrestrial genus *Gecarcinus* are both represented in the Miocene deposits of Œningen.

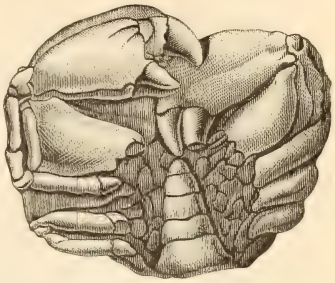

Fig. 429.—*Palæocarpilius macrocheilus.* Eocene.

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CHAPTER XXXI.

ARTHROPODA—continued.

ARACHNIDA AND MYRIOPODA.

Class II. Arachnida.

The *Arachnida*—including the Spiders, Scorpions, Mites, &c.—possess almost all the essential characters of the *Crustacea*, to which they are very closely allied. Thus, the body is divided into a variable number of somites, some of which are always provided with articulated appendages. A pair of ganglia is primitively developed in each somite, and the neural system is placed ventrally. The heart, when present, is always situated on the opposite side of the alimentary canal to the chain of ganglia. The respiratory organs, however, whenever these are differentiated, are never in the form of branchiæ as in the *Crustacea*, but are in the form either of pulmonary vesicles or sacs, or of ramified tubes, formed by an involution of the integument, and fitted for breathing air directly. Further, there are never more than four pairs of ambulatory limbs, and no locomotive appendages are developed upon any of the abdominal segments. Antennæ are not present (as such), and the eyes are simple and sessile. The head and thorax are united to form a cephalothorax (the thoracic segments in rare cases remaining free), and in some cases the cephalothorax is fused with the abdomen.

Speaking generally, therefore, the *Arachnida* are distinguished from the *Crustacea* by *the possession of four pairs of walking-legs, the want of locomotive appendages on the abdomen, and the absence of antennæ; while the breathing-organs (when differentiated) are adapted for breathing air directly, and are never in the form of branchiæ.*

The integument of the *Arachnida* is in general more or less extensively hardened by chitine, and commonly forms a resistant exoskeleton. Viewed under the microscope, the chitinous exoskeleton of such an Arachnidan as a Scorpion (fig. 430, A and B) exhibits a

finely punctate or minutely porous structure, along with numerous oval pits of different sizes, each of which exhibits a central dark spot or ring. These latter are not perforations, but are the sockets of hairs. The skin of a fossil Scorpion from the Carboniferous rocks (collected by the Geological Survey of Scotland) also exhibits a minutely reticulate or porous structure, and presents larger oval pits, which show a central dark spot, and which seem to be quite similar to the hair-sockets of the recent Scorpions (fig. 430, C and D). There are also still larger oval perforations, which are surrounded by a fibrous ring, and which are true *perforations*, passing completely through the thin integument. These may represent the sockets of large bristles, from which the delicate chitinous membrane forming the original floor of the socket (traces of which are still sometimes visible) has disappeared; or they may be truly pores. In the latter case, they do not appear to have any representative in the integument of the recent Scorpions.

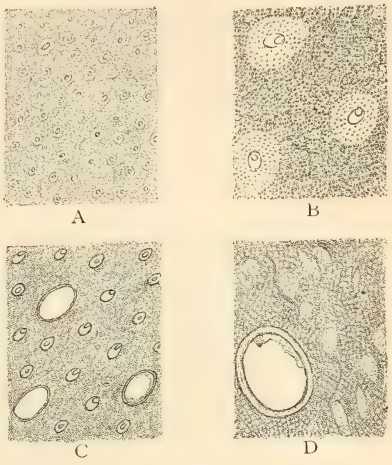

Fig. 430.—A, Exoskeleton of a recent Scorpion enlarged, and (B) still more highly magnified, showing minute pores together with larger pits to which hairs were attached. C, Portion of the skin of a fossil Scorpion from the Carboniferous rocks of Scotland, enlarged, showing pits for the attachment of hairs. The large oval perforations probably also represent the sockets of hairs, of larger size. D, Portion of the same enlarged further, showing a finely reticulate or porous structure. (Original.)

The segments of the head and thorax in the *Arachnida* are generally amalgamated to form a "cephalothorax," which is in some cases (*Solpugidæ*) segmented. The upper surface of the head carries the eyes, which are always simple and are never supported upon movable peduncles. There are no proper "antennæ," but the place of these is taken by a pair of prehensile organs known as the "cheliceræ," "falces," or "mandibles" in different groups of the class (fig. 431, *c*). There is a single pair of "maxillæ" or proper jaws, which carry long jointed appendages—the "maxillary palpi." The palpi are sometimes leg-like in form ("pedipalpi"), or they may, as in the Scorpions, be converted into nipping-claws (fig. 431, *m*). Immediately posterior to the mouth is a lower lip or "labium," which is unpaired in the Spiders, but in some cases is partially divided by a longitudinal groove, and is thus seen to represent a second pair of maxillæ. The four segments of the thorax

carry, as a rule, four pairs of jointed ambulatory legs. Abdominal limbs are present in the embryo of various *Arachnida*, but ambulatory appendages are never developed on the abdominal somites of the adult. In the Scorpions, the first abdominal segment carries a minute "operculum," formed by the coalescence of a pair of appendages, which covers the opening of the reproductive organs; and the second abdominal segment carries the peculiar organs which

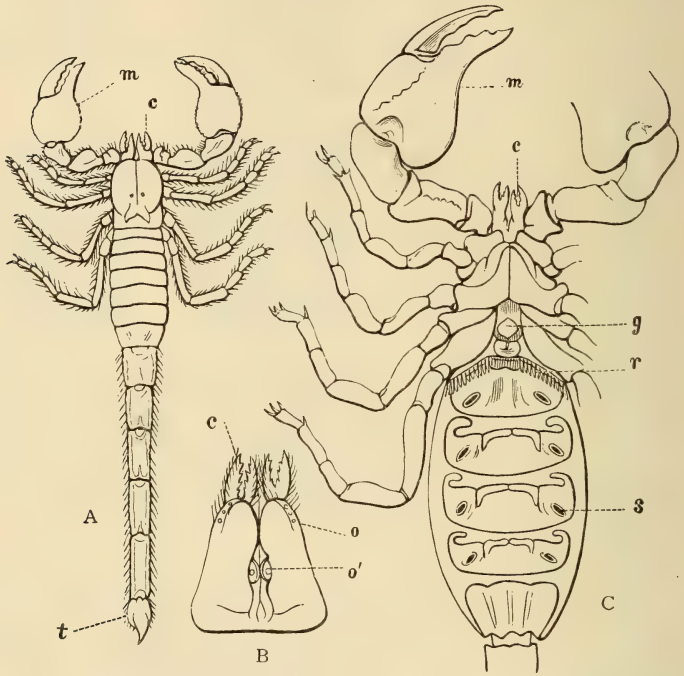

Fig. 431.—A, *Scorpio afer*, viewed from above, and somewhat reduced in size; B, Upper surface of the cephalothorax of the same, enlarged; C, *Buthus Kochii*, with the terminal segments and the ends of the appendages on one side omitted. *m*, Maxillary palpi (behind these are the four pairs of ambulatory legs); *c*, Cheliceræ; *t*, Telson; *o*, Lateral ocelli; *o'*, Central, larger ocelli; *g*, Opercular plate, covering the opening of the reproductive organs; *r*, One of the "combs"; *s*, One of the stigmatic openings. (C is after Prof. Ray Lankester.)

are known as the "combs." The extremity of the abdomen carries in the Spiders the so-called "spinnerets" (two, four, or six in number), which have sometimes been regarded as modified abdominal appendages. A "telson" is present in the Scorpions, in which it forms a poisonous "sting"; and a jointed caudal filament is present in *Thelyphonus*.

The higher *Arachnida* are air-breathers, and possess distinct respiratory organs in the form of "tracheæ" or "pulmonary sacs," the

former being tubular and the latter pouch-like in form. The air is admitted to the breathing-organs by paired apertures ("stigmata"), which are mostly placed on the ventral aspect of the abdomen. Many of the lower *Arachnida* have no differentiated respiratory organs; and the Pycnogonids, if rightly placed in this class, are water-breathers.

As regards their *distribution in space*, the higher *Arachnida* are essentially terrestrial in habit. Many of the lower forms are internal or external parasites. A few of the Mites live in the sea or between tide-marks, and the singular Pantopods (*Pycnogonida*) are wholly marine in habit: but the zoological position of these last is uncertain.

As regards their *distribution in time*, our knowledge of the history of the *Arachnida* is still very incomplete. Many of the lower forms are incapable of preservation, while the terrestrial habits of most of the higher forms sufficiently account for their comparative rarity as fossils. The oldest known representatives of the class are the Scorpions, which appear, under forms not very widely different from those now in existence, in the Silurian rocks. The earliest types of the true Spiders (*Protolycosa* and *Phalaranea*) appear in the Coal-measures, where also appear forms allied to the recent *Thelyphonus*. The great majority of the Palæozoic Arachnids, however, differ in various points from existing forms, and have been placed by Scudder in a special order (*Anthracomarti*), which is confined to the Palæozoic period. In the Mesozoic rocks no undoubted remains of Arachnids have hitherto been detected. On the other hand, in the Tertiary rocks are found representatives of all the living orders of Arachnids, except the problematical group of the *Pycnogonida*, which is not known at all in the fossil state. Most of the Tertiary Arachnids have been found in amber—the fossil resin of certain Conifers—and the state of preservation of these is often marvellously perfect. The more important facts relating to the fossil *Arachnida* may be briefly noticed under the following heads:—

1. Acarida.—This group of the *Arachnida* comprises the Mites and Ticks, in which the cephalothorax and abdomen are fused into a single mass, while the mouth-organs are generally adapted for piercing and suction. Breathing organs may be wanting, but when present, are in form of tracheæ. All the principal existing families of Mites are known to be represented in amber (Tertiary). Galls formed by Mites have also been detected on the leaves of fossil Willows in the Tertiary beds of Europe.

2. Anthracomarti.—This order has been founded for the reception of certain Palæozoic Arachnids, in which the body is somewhat compressed, the cephalothorax and abdomen are distinctly

separated from one another, and the former is usually composed of more or fewer wedge-shaped, foot-bearing segments. The abdomen consists of from four to nine somites, and the "palpi" are not much longer than the legs, and are not terminated by pincers or claws (Scudder). Of the genera included in this extinct group, all of which are confined to the Carboniferous period, *Architarbus* (fig. 432, B) is found in the Coal-measures of both Europe and North America. In *A. subovalis* the cephalothorax is shorter than the abdomen and carries four pairs of legs and a pair of palpi, the form of which is unknown. The abdomen consists of nine seg-

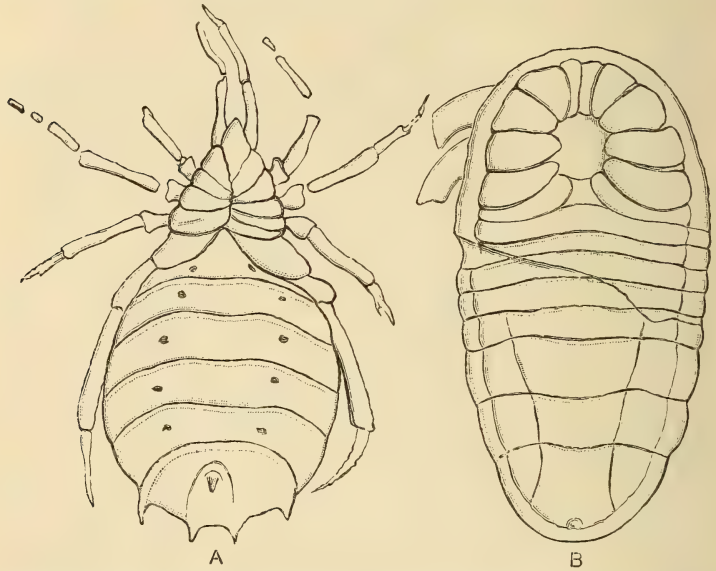

Fig. 432.—A, *Eophrynus Prestvicii*, viewed ventrally, and somewhat enlarged—Carboniferous; B, *Architarbus subovalis*, enlarged four times, and viewed from below—Carboniferous (after H. Woodward).

ments, of which the anterior ones are much narrower than the hinder ones. In *Anthracomartus*, also distributed in the Coal-measures of Europe and North America, the cephalothorax is quadrangular, and is only about half as wide as the abdomen, the latter region consisting of seven segments. In *Arthrolycosa*, from the Coal-measures of Illinois, the cephalothorax, on the other hand, is round, and is much larger than the abdomen, the latter region consisting of seven distinct segments and being comparatively narrow. Lastly, in the singular genus *Eophrynus* (fig. 432, A), the cephalothorax is triangular and extended in front, and carries the four pairs of legs and a pair of slender palpi. The abdomen is twice as large

as the cephalothorax, and its upper surface is tuberculated, while on its ventral aspect are seen the openings of six pairs of stigmata.

3. Adelarthrosomata.—Under this name may be included Arachnidans such as the "Book-scorpions" (*Pseudoscorpionidæ*) and the "Harvest-men" (*Phalangidæ*), in which the abdomen is more or less distinctly segmented, but is not clearly separated from the cephalothorax, the two regions being of equal width and conjoined together; while the respiratory organs have the form of tracheæ. Various Tertiary forms of the Pseudoscorpions have been detected—principally in amber—but these all belong to existing genera (*Chelifer*, *Chernes*, &c.) Of the *Phalangidæ* no other fossil forms are known except those which occur in amber, and of these a number of types, belonging to several genera, have been described.

4. Pedipalpi.—Under this head may be included the two groups of the Scorpions (*Scorpiodea*) and the *Phrynidea*, in which the abdomen is segmented, with or without a "post-abdomen," and the breathing-organs are in the form of pulmonary sacs. The Scorpions are characterised by their compressed bodies, and by the clear separation of the cephalothorax from the long and segmented abdomen. The abdomen proper consists of seven wide somites, of which the first carries on its ventral surface the opening of the generative organs, closed by a delicate lid or operculum (fig. 431, *g*); the second carries a pair of peculiar comb-like appendages ("pectines"), the precise function of which is not known; and the next four exhibit the oblique apertures ("stigmata") of the four pairs of pulmonary sacs. The abdomen proper is followed by six narrower segments, which constitute a "post-abdomen," and of which the last (the "telson") is hooked, and is converted into a poisonous "sting." The cephalothorax is covered by a shield-like carapace, the upper surface of which carries a variable number of simple eyes, one pair of which is larger than the others, and is placed dorsally, while the smaller eyes are marginal. The first pair of cephalic appendages, corresponding with the "falces" of the Spiders, are converted into nipping-claws ("cheliceræ"); the maxillary palpi are very large and end in pincers; and a partially divided lower lip is present. The four thoracic segments carry the four pairs of walking-legs.

The Scorpions possess a resistant chitinous exoskeleton, readily capable of preservation in the fossil condition (see p. 573). It is also probable that some of the more ancient forms were littoral in habit, which would account for the occurrence of their remains in strata of marine origin. The Scorpions are the most ancient group of the *Arachnida*, being represented in the Silurian rocks of both the Old and New Worlds. Various Carboniferous Scorpions are

also known, and these ancient types do not appear to have differed from the living representatives of the group except in comparatively non-essential characters.

The genus *Palæophonus* (fig. 433) has been detected in the Silurian strata of Gotland and of Scotland, and comprises Scorpions which differ from all existing types in the fact that the walking-legs gradually taper to their ends, which terminate in points or simple claws. The maxillary palpi form strong nipping-claws, and the median eye-tubercles are placed not far from the anterior margin of the cephalothorax. The genus *Proscorpius* occurs in the Silurian deposits of North America, and differs from the preceding in the

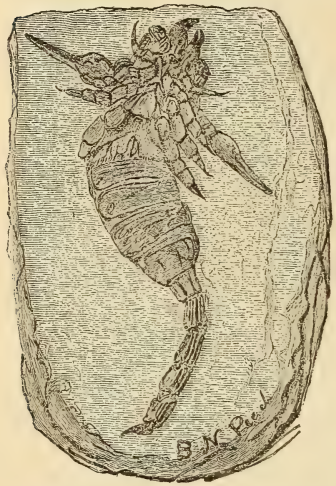

Fig. 433.—Ventral aspect of a species of *Palæophonus*, from the Silurian rocks of Lesmahagow, Lanarkshire. Enlarged nearly twice. (After Benjamin N. Peach.)

Fig. 434.—A specimen of *Eoscorpius carbonarius*, from the Carboniferous rocks of Illinois, of the natural size. (After Meek and Worthen.)

fact that the legs are long, with blunt terminal joints ending in two claws. The median dorsal eye-tubercles are placed on the anterior margin of the cephalothorax, and the lateral eyes are on ridges, as in the living Scorpions. The genus *Eoscorpius* (fig. 434) is confined to the Carboniferous rocks, and species have been detected in the Coal-measures of both Europe and North America. *Mazonia* is probably identical with *Eoscorpius*. The genus is nearly related to *Proscorpius*, from which it differs in having the median dorsal eye-tubercles of smaller size, and not placed close to the anterior margin of the cephalothorax. The Coal-measures of Europe and North America have also yielded the remains of Scorpions on which the genus *Cyclophthalmus*—including the first fossil forms known to

science—was founded. In this genus (fig. 435) the median dorsal eye-tubercles are of very large size, and occupy almost half of the cephalothorax towards the anterior margin, while the lateral eyes form a semicircle behind and to the sides of the great dorsal eyes, and the palpi are developed into nipping-claws of very large size. According to Mr Scudder, the four genera just mentioned constitute a special division of the Scorpions (*Anthracoscorpii*), characterised, among other points, by the fact that the dorsal eye-tubercles are either placed on the anterior margin of the cephalothorax or a short distance behind it. On the other hand, in the Scorpions of the

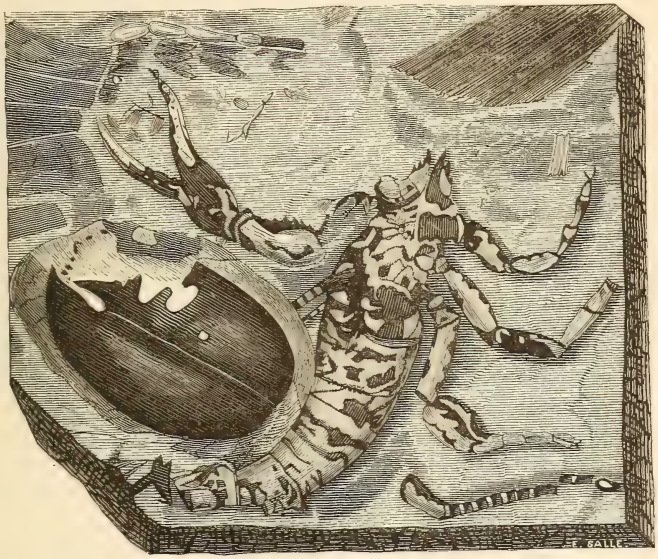

Fig. 435.—*Cyclophthalmus senior.* A fossil Scorpion from the Coal-measures of Bohemia.

more modern type (*Neoscorpii*), the median eye-tubercles are, as a rule, far removed from the anterior margin of the cephalothorax, and are placed behind the lateral eyes. It is a singular fact that while the *Anthracoscorpii* are wholly confined to the Palæozoic rocks, no example of the *Neoscorpii* has hitherto been detected in the Mesozoic or in the earlier Kainozoic deposits. The only known fossil representative of the *Neoscorpii*, in fact, is a late Tertiary form (*Tityus eogenus*) which has been discovered in amber.

The remaining section of the *Pedipalpi* is that of the *Phrynidea*, which differs from the Scorpions in the fact that the cephalothorax is sharply separated from the abdomen, and is occasionally divided into two distinct regions. The maxillary palpi are greatly developed,

but terminate in claws or in imperfect pincers, and the abdomen does not terminate in a "sting." The existing genus *Phrynus* has been detected in Tertiary deposits, while the recent genus *Thelyphonus* is represented in the Carboniferous rocks by the genus *Geralinura*.

5. Araneida.—This division of the *Arachnida* includes the true Spiders, characterised by the soft and imperfectly segmented abdomen, which carries two, four, or six "spinnerets" posteriorly, and is united in front with the cephalothorax by a constricted peduncle. The maxillary palpi are slender and leg-like, and never terminate in nipping-claws, while the "falces" or "mandibles" are hooked, and contain a poison-gland in their base. The most ancient representatives of the Spiders, so far as at present known, are the *Protolycosa anthracophila*, and *Phalaranea borassifolia* of the Coal-measures of Europe, both of which have been referred to the section of the *Territelariæ*. No Mesozoic Spiders have hitherto been discovered; but about seventy genera have been recognised as occurring in Tertiary deposits—many of them in amber. About one-half of the known Tertiary genera of Spiders are without representatives at the present day.

Class III. Myriopoda.

The class of the *Myriopoda* includes the multisegmentate, worm-like Arthropods known as the Centipedes and Millepedes, and is characterised by the fact that *the head is distinct, and the remainder of the body is divided into nearly similar segments, the thorax exhibiting no clear line of demarcation from the abdomen. There is one pair of antennæ, and the number of the legs is always more than eight pairs. Respiration is by tracheæ.*

In this class of the *Arthropoda* the head is always distinctly marked off from the rest of the body, and consists of five or six amalgamated somites. The head carries a single pair of jointed antennæ, which are usually simple (fig. 436), but are bifid, and carry many-jointed appendages in the aberrant genus *Pauropus*. Behind the antennæ there is generally a variable number of simple sessile eyes. The mouth is placed on the under side of the head, and is provided with mandibles and maxillæ. The Centipedes also possess two pairs of "foot-jaws," of which the hindmost pair (fig. 436, *f*) are of large size, and are terminated by perforated hooks, which communicate with internally-placed poison-glands. These appendages, however, are not carried upon the head, but are attached to a special segment formed by the amalgamation of the anterior thoracic rings. The segments behind the head are numerous, and there is no distinct line of demarcation between those

which belong to the thorax and those which are referable to the abdomen. The post-cephalic segments, with the exception of the last, usually carry a single pair of jointed legs each. Among the living Myriopods, *Pauropus* has only nine pairs of legs; but, with this exception, eleven pairs of legs is the smallest number possessed by any existing type. In the Millepedes (*Diplopoda*) each apparent segment carries two pairs of legs (fig. 437); but this is really due to

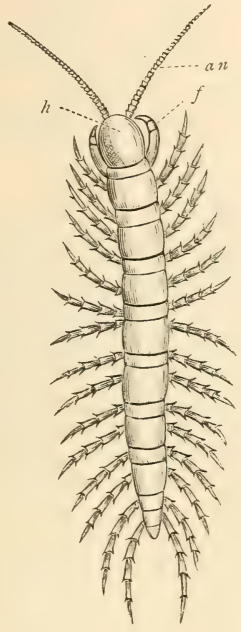

Fig. 436.—*Lithobius forficatus*, a recent Centipede, enlarged, and viewed dorsally. *an*, Antennæ; *h*, Head; *f*, Foot-jaw.

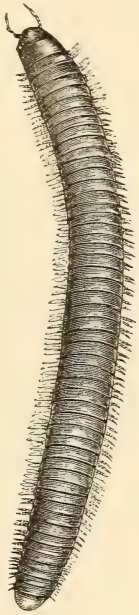

Fig. 437.—*Iulus maximus*, a recent Millepede.

the coalescence of the somites in pairs, each apparent segment being in reality composed of two amalgamated somites.

In the abnormal genus *Pauropus* respiration is cutaneous, but in all other living Myriopods the breathing-organs are in the form of "tracheæ"—that is to say, tubes which open on the surface of the body by minute apertures or "stigmata," and which convey the air into the interior of the body. In *Peripatus* the tracheæ open externally by irregularly placed "stigmata" over the whole surface of the body. In the Centipedes the "stigmata" are placed on the sides of the body on alternate segments. In the Millepedes (*Diplo-*

poda), on the other hand, in which the segments are amalgamated in pairs, the stigmata are placed on every apparent ring.

The recent Myriopods are grouped into the four orders of the *Chilopoda* (Centipedes), *Diplopoda* (Millepedes), *Pauropoda* (*Pauropus*), and *Onychophora* (*Peripatus*). To these Scudder has added the two extinct orders of the *Protosyngnatha* and *Archipolypoda* for the reception of the Palæozoic types of Myriopods.

As regards their distribution in time, all the recent Myriopods are terrestrial in habit. As a necessary result of this, the remains of Myriopods are not abundant as fossils, and have been mostly found in deposits of distinctly fresh-water or estuarine origin. The occurrence of Myriopods in unequivocally marine strata is, however, by no means unknown, though difficult with our present knowledge to satisfactorily explain. The two living orders of the *Pauropoda* and *Onychophora*—represented each by a single genus only—are unknown as fossils, and require no further consideration here. The other two existing orders—viz., the *Chilopoda* and *Diplopoda*—are represented only by Tertiary types, with the possible exception of a Cretaceous form of the latter order. On the other hand, a considerable number of Palæozoic Myriopods are known, which differ more or less widely from all existing types, and for the reception of which Mr Scudder has founded the two orders of the *Protosyngnatha* and *Archipolypoda*. The only known representative of the *Protosyngnatha* is the genus *Palæocampa*, which is found in the Coal-measures of North America. The oldest Myriopods, however, belong to the *Archipolypoda*, and remains of early forms of this order have been described by Mr Peach as occurring in the Old Red Sandstone of Scotland. It is, however, in the Carboniferous rocks that this ancient group of Myriopods attains its maximum development, about thirty different species having been already described from the Coal-measures of the Old and New Worlds. There are also a few Myriopods known to occur in the Permian rocks of Europe, which probably belong to the same order. In the following a brief account is given of the four orders of Myriopods which are known to be represented by fossil forms.

Order I. Protosyngnatha.—This order comprises only the single genus *Palæocampa*, of which only a single species (*P. anthrax*) has been hitherto recorded. In this remarkable genus (fig. 438) the body is comparatively short and worm-like, consisting of few segments, each body-ring being furnished with a single dorsal and ventral plate. Each segment carries a pair of stout fleshy legs, and the upper surface is furnished with large tubercles, each of which supports a cluster of long needles, and which are arranged in longitudinal rows. The sole known species of *Palæocampa* is found in the Coal-measures of Illinois; and the possession of the bundles

of long bristles above mentioned gives to the fossil the aspect of the caterpillar of such a Moth as the Tiger-moth.

Order II. Chilopoda.—This order includes the recent Centipedes (fig. 436), characterised by their elongated depressed bodies, each body-ring being protected by a dorsal plate above, and a corresponding ventral plate below. The first two pairs of thoracic appendages are converted into foot-jaws, the second pair being of large size and hooked, and being connected with poison-glands. All the remaining body-rings carry a single pair of jointed legs each, and the tracheal stigmata are usually placed on alternate segments. The generative organs open at the posterior end of the body.

With the exception of the problematical *Geophilus proavus* of the Lithographic Slates (Jurassic) of Germany, the oldest known

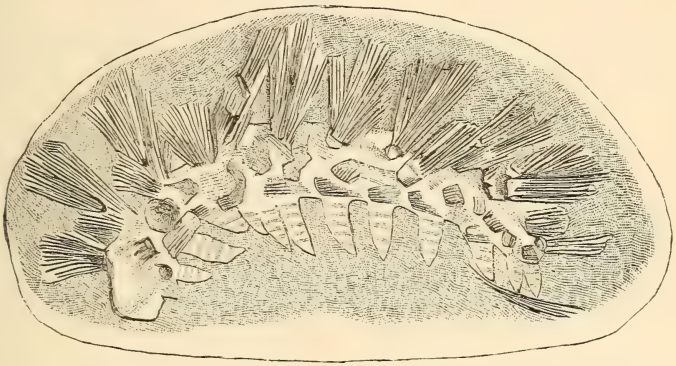

Fig. 438.—A specimen of *Palæocampa anthrax*, from the Coal-measures of Illinois, enlarged twice. (After Scudder.)

remains of Centipedes are of Tertiary age. Most of these have been found in amber, and they all fall under existing families of the order.

Order III. Archipolypoda.—This order has been founded by Scudder for the reception of a number of Palæozoic Myriopods, and is characterised as follows: The body in the *Archipolypoda* is fusiform and elongated, composed of many segments, and thickest in the anterior half or third. The cephalic appendages are borne upon a single apparent segment. The body-segments are provided each with a pair of ventral plates and a more or less divided dorsal plate, "the latter occupying the upper surface and most of the sides of the body, and divided more or less conspicuously into a ridged anterior and a lower posterior portion, the anterior frequently bearing spines or tubercles." The ventral plates are as broad as the body, each bearing a pair of long corneous legs, approximated at the base, and

furnished outside the legs with large stigmata directed transversely to the axis of the body (Scudder). This order comprises all the Palæozoic *Myriopoda* with the exception of the Carboniferous genus *Palæocampa*, and it is not known to have any representatives in the Mesozoic or Kainozoic rocks. The most ancient types of the *Archipolypoda* at present known are those recorded by Page and Peach as occurring in the Old Red Sandstone of Scotland (*Kampecaris* and *Archidesmus*). With these exceptions, all the members of the order are either Carboniferous or Permian in age. The three most important genera of the *Archipolypoda* are *Euphoberia*, *Archiulus*, and *Xylobius*. In the genus *Euphoberia* (fig. 439) the dorsal shields are divided each into two more or less closely consolidated, but distinctly separate sub-segments, one of which is much more elevated than the other. The segments are generally from two to three times broader than long, and they carry subdorsal and lateral rows of large spines, which are forked and terminate in simple ends. The species of *Euphoberia* are found in the Coal-measures of North

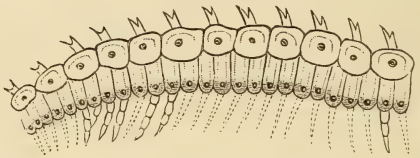

Fig. 439.—Portion of the body of *Euphoberia armigera*, from the Coal-measures of Illinois, of the natural size (after Meek and Worthen). The dark spots on the dorsal shields are pits left by the breaking off of the dorsal spines.

America and Britain. The genus *Acantherpestes* includes Carboniferous Myriopods which differ from *Euphoberia* chiefly in having the spines bifurcated at the tip, though there are other characters of difference as well. *Acantherpestes major*, of the Coal-measures of Illinois, attained a length of about a foot, and "was armed with coarse branching spines more than a centimetre long" (Scudder). Mr Scudder regards this species as having been amphibious in habit, as he considers that certain lateral openings which it exhibits were branchial in character.

The genera *Archiulus* and *Xylobius* constitute a special family (*Archiulidæ*) of the *Archipolypoda*, characterised by the fact that the dorsal plates are "closely consolidated, but still distinctly separable," though the anterior is rarely much elevated above the posterior sub-segment. The body is "almost smooth or covered more or less abundantly with serially disposed papillæ, from which in some cases hairs or small spines arise" (Scudder). These genera are closely allied in some respects to the Millepedes (*Diplopoda*), though they would seem on the whole to be properly referable to a

separate order. In *Archiulus* the dorsal plates are entire, generally from two to three times broader than long, and furnished with a few bristle-bearing papillæ. The best known species of this genus have been found in the Coal-measures; but some imperfectly described Myriopods from the Permian rocks of Bohemia may also belong here. The genus *Xylobius* resembles *Archiulus* in general features, but the segments are divided by longitudinal sutures into numerous quadrate sections. All the known species of this genus are from the Coal-measures.

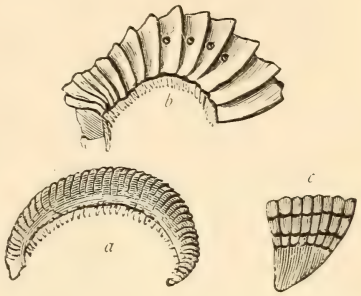

Fig. 440.—*Xylobius Sigillariæ*, a Carboniferous Myriopod (after Dawson). *a*, Natural size; *b*, Anterior portion, enlarged; *c*, Posterior portion, enlarged.

Order IV. Diplopoda (Chilognatha).—This order includes the recent Millepedes, and is characterised by the fact that the body is usually cylindrical, and the body-rings (except the most anterior ones) are fused in pairs, each apparent segment thus coming to carry two pairs of legs. The legs are small and spring from the under surface of the segments, and each apparent ring carries a pair of stigmata. There are no "foot-jaws," and the generative apertures are placed anteriorly, at the base of the second or third pair of legs.

The oldest known fossil representative of the *Diplopoda* is a form (*Iulopsis cretacea*) which has been described from the Cretaceous rocks of Greenland. All the other hitherto recorded fossil Millepedes are of Tertiary age, the majority of the known types having been found in amber.

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CHAPTER XXXII.

ARTHROPODA — continued.

Class IV. Insecta.

The *Insecta* are defined as *Articulate animals in which the head, thorax, and abdomen are distinct; there are three pairs of legs borne on the thorax; the abdomen is destitute of legs; a single pair of antennæ is present; mostly, there are two pairs of wings on the thorax. Respiration is effected by tracheæ.*

The integument of the *Insecta*, in the mature condition, is more or less hardened by the deposition of chitine, and usually forms a resisting exoskeleton, to which the muscles are attached. The segments of the head are amalgamated into a single piece, which bears a pair of jointed feelers or antennæ, a pair of eyes, usually compound, and the appendages of the mouth. The segments of the thorax are also amalgamated into a single piece; but this, nevertheless, admits of separation into its constituent three somites (fig. 441). These are termed respectively, from before backwards, the "prothorax," "mesothorax," and "metathorax," and each bears a pair of jointed legs. In the great majority of Insects, the dorsal arches of the mesothorax and metathorax give origin each to a pair of wings.

Each leg consists of from six to nine joints. The first of these, which is attached to the sternal surface of the thorax, is called the "coxa," and is succeeded by a short joint, termed the "trochanter." The trochanter is followed by a joint, often of large size, called the "femur," succeeded by the so-called "tibia," and this has articulated to it the "tarsus," which may be composed of from one to five joints.

The wings of Insects are expansions of the sides of the meso- and meta-thorax, these expansions being supported by slender but firm tubes, known as the "nervures." Each nervure consists of a central trachea or air-tube, running in the centre of a larger blood-tube;

so that the wings not only act as organs of flight, but at the same time assist in the process of respiration. Normally, two pairs of wings are present, but one or other may be wanting.

The arrangement of the "nervures" of the wings is definite and characteristic in different groups of the Insects. In the most typical forms of wing, as in the *Orthoptera* (fig. 442, A), there are six principal veins, which arise, in groups of three, from two principal roots, one anterior and the other posterior. According to the nomenclature followed by Heer and Scudder, these six principal veins are termed, from before backwards, the *marginal*, *mediastinal*, *scapular*, *externomedian*, *internomedian*, and *anal* veins. The general arrangement of these veins (fig. 442, A) is as follows: "The *marginal* vein (*ma*) is placed at, or close to, the anterior margin of the wing; and "the 'mediastinal' and 'scapular' veins, which are superior (*i.e.*, part from the main vein on the upper or anterior side), terminate upon the anterior margin. The 'internomedian' and 'anal' take the opposite course, and their branches are inferior, or, at least, directed towards the inner margin; while the 'externomedian,' which is interposed between these two sets, terminates at the tip of the wing, and branches indifferently on either side" (Scudder). In some groups of the Insects there may be a suppression of certain of these six primary veins, and the above general arrangement is liable to characteristic modifications in different cases. The value of the characters derived from the neuration of the wings is, however, impaired by the fact that entomologists have not adopted a uniform nomenclature of the nervures in different orders of the *Insecta*.

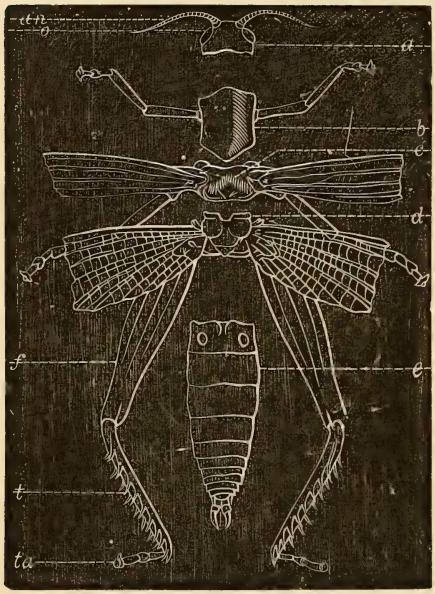

Fig. 441.—Diagram of the external anatomy of an Insect. *a*, Head carrying the eyes (*o*) and antennæ (*an*); *b*, First segment of the thorax, with the first pair of legs; *c*, Second segment of the thorax, with the second pair of legs and the first pair of wings; *d*, Third segment of the thorax, with the third pair of legs and the second pair of wings; *e*, Abdomen, without limbs, but carrying terminal appendages concerned in reproduction; *f*, Femur; *t*, Tibia; *ta*, Tarsus.

In the *Coleoptera* (Beetles) the wings of the anterior pair become

hardened by the deposition of chitine, so as to form two protective cases for the hinder membranous wings. In this condition the anterior wings are known as the "elytra," or "wing-cases." In some of the *Hemiptera* this change only affects the inner portions of the anterior wings, the apices of which remain membranous, and

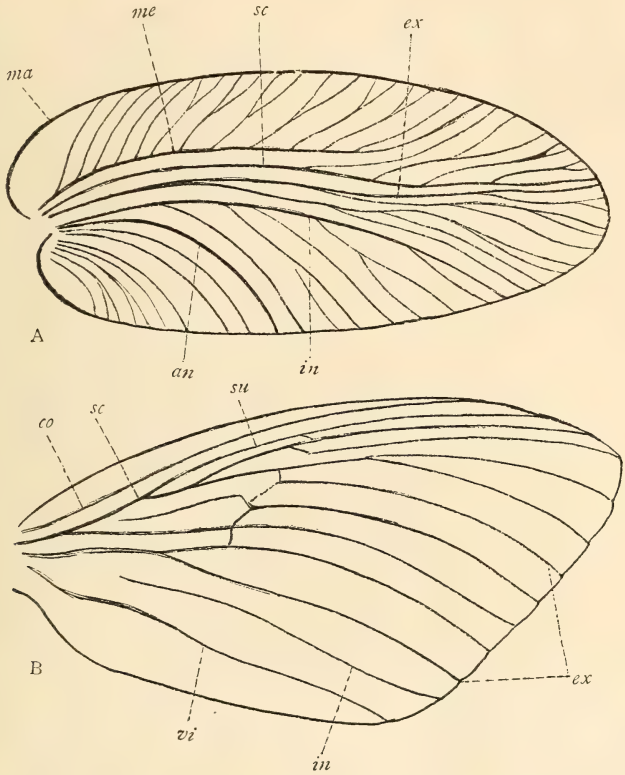

Fig. 442.—A, Schematic view of the right anterior wing of a Palæozoic Cockroach, greatly enlarged. (After Scudder.) *ma*, "Marginal" vein, which in this case merely thickens the margin of the wing; *me*, "Mediastinal" vein; *sc*, "Scapular" vein; *ex*, "Externomedian" vein; *in*, "Internomedian" vein; *an*, "Anal" vein. B, Anterior wing of Butterfly (*Castnia veraguana*), enlarged; *co*, "Costal" vein; *su*, "Subcostal" vein; *sc*, "Scapular" vein; *ex*, Branches of the "externomedian" vein; *in*, "Internomedian" vein; *vi*, "Internal" vein. (After J. O. Westwood.)

to these the term "hemelytra" is applied. In the *Diptera* the posterior pair of wings are rudimentary, and are converted into two capitate filaments, called "halteres" or "balancers." In the *Strepsiptera* the anterior pair of wings are rudimentary, and are converted into twisted filaments.

The typical number of somites in the abdomen of the *Insecta* is ten or eleven, and this number can sometimes be recognised in the *Orthoptera* and some other forms. In the *Hymenoptera* and *Lepidoptera* not more than nine or ten can be recognised, and in many cases even fewer can be made out. The abdominal somites are usually more or less freely movable upon one another, and never carry locomotive limbs. The extremity of the abdomen is, however, commonly furnished with appendages, which are connected with the generative function, and not infrequently serve as offensive and defensive weapons. Of this nature are the ovipositors of Ichneumons and other insects, and the sting of Bees and Wasps. In the Earwig (*Forficula*) these caudal appendages form a pair of forceps; whilst in many insects they are in the form of bristles, by which powerful leaps can be effected, as is seen in the Spring-tails (*Podurœ*).

Generally speaking, the young insect is very different in external characters from the adult, and it requires to pass through a series of changes, which constitute the "metamorphosis," before attaining maturity. In some Insects, however, there appears to be no metamorphosis, and in some the changes which take place are not so striking or so complete as in others. By the absence of metamorphosis, or by the degree of its completeness when present, Insects are divided into sections, called respectively *Ametabola*, *Hemimetabola*, and *Holometabola*, which, though not, perhaps, of a very high scientific value, are nevertheless very convenient in practice.

The "Ametabolic" Insects are those which have no proper "metamorphosis," the young stages of the Insect resembling the adult in all essential points except in size. This absence of a metamorphosis is only seen in Insects which are destitute of wings in the adult condition, and which are therefore often spoken of as the *Aptera*. In the so-called "Hemimetabolic" Insects, where an "incomplete" metamorphosis exists, the young insect is at first very different from the adult, and in the process of conversion into the latter it undergoes changes of form, while it at the same time remains capable of locomotion and of nourishing itself. In its first condition, after emergence from the egg, it is known as a "larva," and at this stage it presents no traces of wings. In its second condition—the stage of the "pupa"—it possesses rudimentary wings, but is still active and feeds. In its third stage, as the perfect insect or "imago," the wings are fully developed, and the insect acquires the power of flight. Lastly, the Insects which undergo a "complete" metamorphosis, and which are therefore said to be "holometabolic," pass through the same series of changes as those observed in the case of the Hemimetabolic forms, but the larva, pupa, and imago differ from one another more widely than is the case in the latter, and the insect in the "pupa" stage is quiescent and does not feed.

The great majority of existing Insects are terrestrial in habit, and almost all of those which are aquatic are inhabitants of fresh water. For these reasons, the remains of Insects are by no means abundantly preserved in the fossil condition, and are chiefly found in association with deposits of coal, or in lacustrine or fluviatile strata. Moreover, the remains of this class of Arthropods are generally found (except when preserved in amber) in a more or less fragmentary condition, and, under any circumstances, they cannot be satisfactorily deciphered except by practised workers in the department of Entomology. Between two and three thousand species of fossil Insects have been already described, but for the reasons just stated, it would be impossible here to deal with these in even a very general manner. The student desirous of acquiring a detailed knowledge of the fossil Insects must have recourse to special works on the subject, and, especially, to the admirable treatises published by Mr Scudder (see 'Literature of Insecta'). All that can be attempted here is to give a brief outline of the general geological distribution of the class, and of the leading characters and range in time of the great orders of *Insecta*.

As regards the general geological distribution of the *Insecta*, the oldest known insect is the *Palæoblattina Douvillei*, recently described by Brongniart from rocks belonging to the inferior portion of the Silurian (Upper Silurian) rocks of France. With the exception of this ancient type, the earliest remains of Insects are found in the Upper Devonian rocks of North America. "It is, however, only when we reach the productive Coal-measures that we arrive at insect-faunas of considerable extent, such as those especially of Commentry in France and of Mazon Creek in Illinois. Other considerable deposits are found in the Coal-fields of the Saarbrück and Wettin basins of Germany, the Belgian and British Coal-fields, and in America the Coal-basins of Nova Scotia and Pennsylvania. The Permian offers comparatively few species, but some of these are of particular interest (*e.g.*, *Eugereon*), and the Trias is almost wanting in fossil insects, except in the South Park of Colorado, where about twenty species have recently been obtained, affording transitional forms among the Cockroaches. Later Mesozoic deposits have yielded nothing in America, but much in England, where nearly all the strata from the Lower Lias to the Wealden have been productive. On the Continent of Europe prolific Liassic deposits have been discovered at Dobbertin in Germany and Schambelen in Switzerland, while the Oolitic beds of Solenhofen are world-renowned. Scanty returns have come from the Cretaceous, but the early Tertiaries have yielded an abundant harvest in the amber deposits of the Baltic shore, the marls of Aix, and in America at Florissant and Green River, while the Middle Tertiaries of Oeningen, Radoboj,

Parschlug, and Auvergne, and the Rhenish Brown Coals have been scarcely less prolific" (Scudder).

All the known Palæozoic Insects are referred by Mr Scudder to "a single homogeneous group of generalised Hexapods," which this eminent authority has named *Palæodictyoptera*, and which "should be separated from later types more by the lack of those special characteristics which are the property of existing orders than by any definite peculiarities of its own." With the exception of a few forms from the Trias of North America, which are allied to the Cockroaches, all the types included by Scudder under the name of *Palæodictyoptera* are restricted to the Palæozoic period. Of the modern orders of Insects, the great divisions of the *Orthoptera*, *Neuroptera*, and *Coleoptera* possess representatives in rocks of Triassic age; while the *Hemiptera*, *Diptera*, *Lepidoptera*, and *Hymenoptera* existed under well-marked forms in the Jurassic period.

In the following brief summary of the orders of Insects, with more especial reference to their geological history, Mr Scudder's treatise on fossil Insects in Zittel's 'Handbuch der Palæontologie' has been followed, with some variation as to the classification adopted :—

Division A. Ametabolic Insects.

Of the four existing orders of Ametabolic or Apterous Insects,—viz., the *Anoplura* ("Lice"), *Mallophaga* ("Bird-lice"), *Collembola* ("Springtails"), and *Thysanura*,—only the last two are known to be represented by fossil forms, and these only in deposits of Tertiary age. Thus, forms allied to the existing *Podura* and *Smynthurus* have been recorded as occurring in amber (early Tertiary), while a species of the recent genus *Lepisma* has been similarly preserved, along with a number of other allied but extinct types. The Oligocene deposits of Florissant, Colorado, have also yielded examples of insects belonging to the order *Thysanura*.

Division B. Hemimetabolic Insects.

Order I. Palæodictyoptera.—This order has been founded by Mr Scudder for the reception of a number of Palæozoic and a few Triassic Insects, with the following characters: "Body generally elongated, mouth-parts variously developed; antennæ filiform. Thoracic joints subequally developed; legs moderately long. Mesothoracic and metathoracic wings closely similar, equally membranous; the six principal veins (fig. 442, A) always developed, the marginal simple, and forming the costal border, the mediastinal simple, or with superior branches only; the other veins usually

dichotomise; stout and well-defined cross-veins rare; membrane generally reticulate. Wings in repose lying on the abdomen, the anal area of the hind-wings, though usually of great distal extension, never plaited, though sometimes broadly folded. Abdomen usually long and slender, the last joint often furnished with simple articulated appendages" (Scudder).

The *Palæodictyoptera*, as above defined, comprise generalised Insects, in which there was an "incomplete" metamorphosis, and the four wings were membranous, equally developed, and characterised by a simple type of neuration. Mr Scudder recognises within the limits of the *Palæodictyoptera* four principal types of structure, representing the existing orders of the *Orthoptera*, *Neuroptera*, *Hemiptera*, and *Coleoptera*, and in accordance with this he has divided the order into four primary groups (the Orthopteroid, Neuropteroid, Hemipteroid, and Coleopteroid groups). The earliest known form of the *Palæodictyoptera* is the *Palæoblattina Douvillei* of the Silurian rocks of Calvados, which is at present the most ancient representative of the entire class of the Insects, and the affinities of which are uncertain. Other forms of the order appear in the Upper Devonian rocks of North America; numerous Carboniferous and a few Permian forms are known; and the last representatives of the order appear in the Triassic rocks of North America.

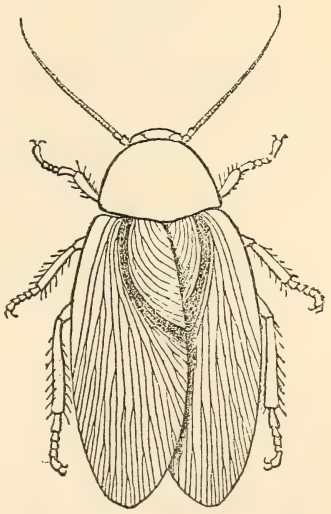

Fig. 443.—*Progonoblattina helvetica*, an Orthopteroid type of the *Palæodictyoptera*, from the Carboniferous rocks of Switzerland, restored. (After Heer.)

The Orthopteroid section of the *Palæodictyoptera* includes a group of forms representing the modern Cockroaches, and a second group which shows relationships to the existing "Stick-insects" (*Phasmidæ*). Apart from the Silurian genus *Palæoblattina*, various Carboniferous types are known which are allied to the existing Cockroaches, but differ from these in the neuration of the wings; and upon such have been founded the genera *Archimylacris*, *Mylacris*, *Progonoblattina* (fig. 443), *Etoblattina*, &c. Of these, the last-mentioned genus occurs also in the Trias of North America, along with other allied forms. The precursors of the modern *Phasmidæ* are the "Protophasmids" of the Carboniferous rocks, comprising various genera which resemble the existing "Stick-insects" in the form of

the body, but in which the wings have the characteristic features of those of the *Palæodictyoptera* generally, being equally developed, with a simple neuration, the anterior pair being unthickened and transparent. The two best known genera of this group are *Titano-*

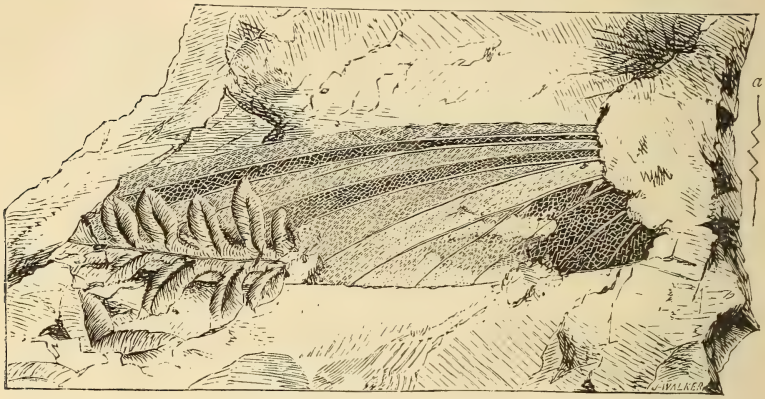

Fig. 444.—*Haplophlebium Barnesii* (after Dawson). From the Carboniferous rocks of Canada. *a*, Profile of base of wing.

phasma and *Protophasma*, both from the Carboniferous rocks. The same formation has also yielded a number of other allied types, upon which have been founded the genera *Dictyoneura*, *Haplophlebium* (fig. 444), *Paolia*, *Breyeria*, &c.

The Neuropteroid section of the *Palæodictyoptera* includes a number of Palæozoic insects, which appear upon the whole to be most nearly allied to the existing May-flies (*Ephemeridæ*). The most ancient types of this section appear in the Upper Devonian rocks of Canada, and upon these have been founded the genera *Platephemera* (fig. 445), *Homothetus*, *Xenoneura*, and *Lithentomum*. A number of allied types, which have been referred to such genera as *Miamia*, *Lithomantis*, *Hemeristia*, &c., have been detected in the Coal-measures of both Europe and North America.

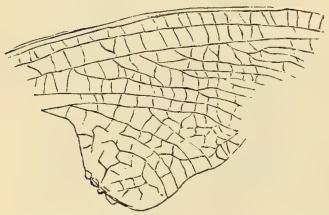

Fig. 445.—Wing of *Platephemera antiqua*, from the Upper Devonian rocks of Canada. (After Dawson.)

Of the Hemipteroid section of the *Palæodictyoptera* the most remarkable type is the Permian genus *Eugereon* (fig. 446). In this remarkable genus the mouth-organs are lancet-shaped, the antennæ are slender and many-jointed, and the front and hind wings are

of large size, transparent, and essentially similar in form and neuration. The Permian genus *Fulgorina* is allied to the preceding; whereas in the *Phthanocoris* of the Coal-measures, the front wings differ in character from the hind wings, and assume the features of "hemelytra."

Lastly, Mr Scudder forms a section of "Coleopteroid" *Palæodictyoptera* for the reception of Palæozoic insects, which may be regarded as precursors of the modern Beetles (*Coleoptera*), and

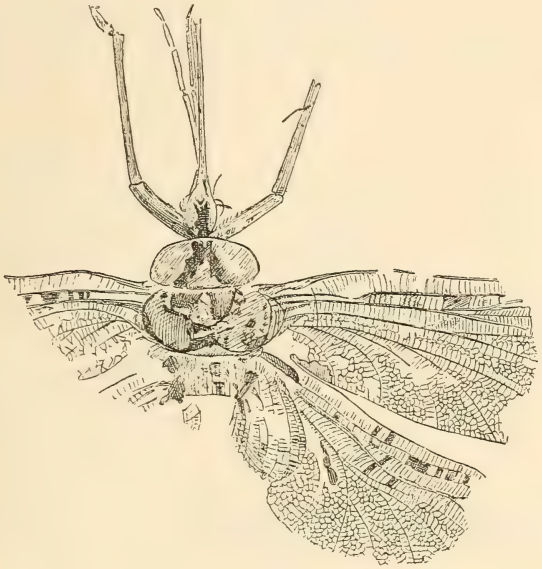

Fig. 446.—*Eugereon Böckingi*, from the Lower Permian rocks of Germany. (After Dohrn—copied from Zittel)

which resemble the latter in having the anterior pair of wings hardened by chitine so as to form cases ("elytra") for the protection of the membranous hind-wings. The existence of insects of this type in the Carboniferous period is shown by the presence in fossil wood from the Coal-measures of borings similar to those produced by existing Beetles. The elytra of Coleopteroid insects have also been recently discovered in the Carboniferous rocks of Silesia, but the characters of these have not yet been fully determined.

Order II. Rhynchota (*Hemiptera*).—*Mouth suctorial, beak-shaped, consisting of a jointed rostrum, composed of the elongated labium and labial palpi, which together form a jointed, tubular sheath*

for the bristle-shaped, styliform mandibles and maxillæ. Eyes compound, usually with ocelli as well. Two pairs of wings in most; sometimes wanting. Pupa generally active.

The recent *Rhynchota* are of very varied habit, and they may be divided into two principal sections in accordance with the structure of the wings. In one great section of the order (*Homoptera*) the anterior and posterior wings are both membranous, the former being simply of firmer texture than the latter. To this section belong such existing types as the Aphides, the Cicadas (fig. 447, C), the Lantern-flies, &c. In the other great section of the order (*Heteroptera*) the anterior wings are hardened at their bases by chitine and remain membranous towards their apices (fig. 447, B), constituting

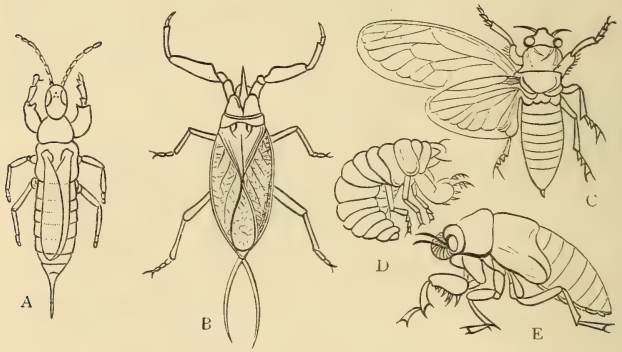

Fig. 447.—Recent Rhynchota. A, *Thrips*, enlarged; B, *Nepa cinerea*, enlarged; C, *Cicada Anglica*, the wings on the right side of the body being omitted; D, Larva of the same; E, Pupa of the same. (Figs. C, D, and E are after Westwood.)

protective cases ("hemelytra") for the wholly membranous hind wings. In this section are included the numerous forms of Land-bugs and Water-bugs.

As regards their geological distribution, the place of the *Rhynchota* in the Palæozoic rocks is taken by the Hemipteroid forms of the *Palæodictyoptera*. In the Jurassic rocks, however, appear for the first time well-marked representatives of both the above-mentioned sections of the order; the Homopterous forms being represented by types allied to the Cicadas, while the Heteropterous division is represented by forms closely allied to, or identical with, the existing Water-scorpions (*Nepa*) and the Land-bugs. The little Plant-lice (*Aphis*, &c.) appear in the Cretaceous rocks (Wealden); and a vast number of Tertiary types of the *Rhynchota* have been described, most of these presenting no marked peculiarities as compared with living types. The *Palæontina oolitica* of the Stonesfield Slate of

England, regarded by Mr Butler as being a Butterfly, is considered by Mr Scudder as truly a Cicada.

Order III. Orthoptera.—In this order *the mouth is masticatory; the wings are four, sometimes wanting, the anterior pair mostly smaller than the posterior and of a semi-coriaceous or leathery consistence. The posterior wings, when not in use, are plaited longitudinally like a fan or may be transversely folded. The interspaces between the nervures are filled with transverse reticulations, and the anal area of the wing is of large size. The antennæ are usually filiform, and the females are usually provided with an ovipositor.*

The earliest types of the *Orthoptera* appear in the Trias, where the order is represented by several forms of Cockroaches. In the Jurassic rocks are found forms belonging to the families of the Earwigs (*Baseopsis*, of the Lias), the Locusts (*Gryllacris* and *Locusta*), and the Crickets (*Gryllus*), while the Grasshoppers (*Acrididæ*) are doubtfully represented in deposits of Mesozoic age. All the preceding families continue to be well represented in the Tertiary rocks, and in deposits of this age appear also forms belonging to the families of the *Mantidæ* and *Phasmidæ*.

Order IV. Neuroptera.—*Mouth usually masticatory; wings four in number, all membranous, generally nearly equal in size, traversed by numerous delicate nervures, which have a longitudinal and transverse direction, thus giving them a reticulated, lace-like aspect* (fig. 448). *Metamorphosis in some groups incomplete, in other groups complete. The larva active, hexapod, the pupa active or quiescent.*

The insects included in the order *Neuroptera* differ so widely in their characters, habits, and metamorphoses that they may be divided into the three primary groups of the *Pseudoneuroptera*, the *Neuroptera vera*, and the *Trichoptera*, of which the first constitutes a transitional group between the typical *Neuroptera* and the *Orthoptera*.

The *Pseudoneuroptera* are characterised by their incomplete metamorphosis, the larvæ being commonly inhabitants of water, and the pupæ being active. Of the groups included in this section of the order, the Termites or "White Ants" are represented in rocks as old as the Lias, and abounded in Tertiary times. The May-flies (*Ephemeridæ*) and the Dragon-flies (*Libellulidæ*) likewise commenced their existence in the Jurassic rocks, and have many Tertiary representatives. Beautifully preserved examples of the Dragon-flies have been yielded by the fine-grained Lithographic Slates of Solenhofen (fig. 448), while still older forms have been recognised in the Lias. Lastly, the family of the *Perlidæ*, including the recent "Stone-flies," is represented in the Eocene Tertiary.

The group of the *Neuroptera vera* includes those members of

the order in which there is a complete metamorphosis, the pupa being inactive, and comprises the Ant-lions (*Myrmeleontidæ*), the Aphis-lions (*Hemerobiidæ*), the Scorpion-flies (*Panorpidæ*), and the *Sialidæ*. The first of these groups is doubtfully known by fossil forms in the Tertiary rocks, but the three last have representatives in the Jurassic rocks, and are also found more or less abundantly in deposits of Tertiary age.

Lastly, the group of the *Trichoptera* comprises the Caddis-flies (*Phryganeidæ*), in which the anterior wings are generally hairy, the larvæ are aquatic and usually reside in tubular cases formed of

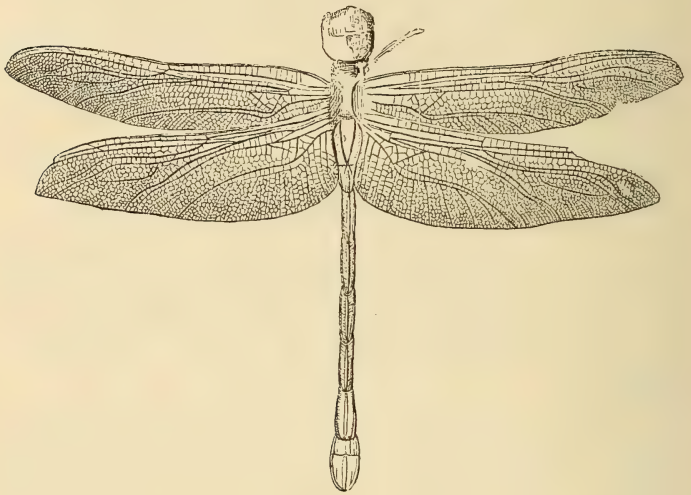

Fig. 448.—*Petalia longialata*, a fossil Dragon-fly from the Lithographic Slates (Jurassic) of Solenhofen. (Copied from Scudder and Zittel.)

small foreign bodies, and the pupæ are inactive during the greater part of their life. A few Mesozoic forms of the Caddis-flies are known, and various Tertiary types have been recognised. The principal palæontological interest of the Caddis-flies arises, however, from the fact that the tubular cases of the larvæ, formed of small fragments of stone or of minute shells cemented together, are capable of preservation in the fossil state. Such cases have been found in the Cretaceous rocks of Bohemia and in various Tertiary deposits, and they sometimes occur in such numbers as to give rise to deposits of considerable thickness. Of this nature is the so-called "Indusial Limestone" of Auvergne, which covers considerable areas, and attains a thickness of eight or ten feet.

Division C. Holometabolic Insects.

Order I. Aphaniptera.—*Wings rudimentary, in the form of scales situated on the mesothorax and metathorax. Mouth suctorial. Metamorphosis complete.*

This order includes only the Fleas, and requires no further consideration here, since no fossil representatives of the group are known to exist.

Order II. Diptera.—This order includes the "Two-winged Flies," and is characterised by the fact that *the mouth is suctorial and is also adapted for piercing; the anterior wings are membranous, with a small basal lobe* ("*alula*"), *not closely reticulated, but with a few, definitely-placed cross-veins. The posterior wings are rudimentary, and are represented by a pair of clubbed filaments* ("*halteres*").

As regards the distribution of the *Diptera* in time, a few representatives of the order have been detected in rocks as old as the Jurassic, but the majority of the fossil forms are found in Tertiary deposits, being especially abundant in amber. Most of the existing families of *Diptera* are represented by fossil forms, but none of these present any points of special interest.

Order III. Lepidoptera.—This order includes the Butterflies and Moths, and is characterised by the fact that *the mouth of the adult is completely adapted for suction, the mandibles being rudimentary. Both pairs of wings are present, and are membranous, being covered with rows of flattened hairs or scales. The neuration of the wings* (fig. 442, B) *is simple, the nervures being rarely united by cross-veins. The "marginal" vein is wanting; while the "scapular" and "externomedian" veins generally form between them a median cell, and give origin to most of the secondary nervures. The metamorphosis is complete, the larva* ("*caterpillar*") *being worm-like, and the pupa* ("*chrysalis*") *being completely enclosed in a horny integument.*

As regards their distribution in time, undoubted remains of several species of *Lepidoptera* (such as the *Sphinx Snelleni* of the Solenhofen Slates) have been detected in the Jurassic rocks; and the tunnels of the larvæ of small Moths have been noticed in fossil leaves of Cretaceous age; but the number of recognised Mesozoic Lepidoptera is very limited. In the Tertiary rocks the remains of *Lepidoptera* are still exceedingly rare, but both the Moths and the Butterflies are now represented by fossil forms. About a dozen Tertiary species of Butterflies are known altogether, and most of these belong to extinct genera (*Mylothrites*, *Neorinopsis*, &c.)

Order IV. Hymenoptera.—This order includes the Ants, Bees and Wasps, Gall-flies, &c., and is characterised by the fact that *the mouth-organs are adapted partly for suction and partly for biting, the mandibles being well developed. Both pairs of wings are usually*

present, the front pair being larger than the hinder pair. The wings are membranous, with a few distant nervures, which are generally connected by cross-veins so as to form large polygonal cells. The females usually with an ovipositor, which may be converted into a "sting" (*aculeus*).

As regards their distribution in time, very few fossil forms of the *Hymenoptera* are known in deposits older than the Tertiary. Of the very limited number of Mesozoic forms one of the most ancient is the *Palæomyrmex prodromus*, described by Heer from the Liassic rocks of Switzerland, which belongs to the family of the Ants (*Formicidæ*), a family which has also representatives in later Jurassic deposits. In the Tertiary rocks the remains of *Hymenoptera* are more abundant, almost all the existing families of importance being represented; but none of the fossil forms are of special interest.

Order V. Strepsiptera.—*Females without wings or feet, parasitic. Males possessing the posterior pair of wings, which are large, membranous, and folded longitudinally like a fan. The anterior pair of wings rudimentary, represented by a pair of singular twisted organs. Jaws rudimentary.*

The *Strepsiptera* constitute a small order, which includes certain minute parasites of Bees and other *Hymenoptera*. The females are grub-like, but the males are winged. A single example of one of the winged males of this singular group of insects has been detected in amber, and has been referred to the extinct genus *Triæna*.

Order VI. Coleoptera.—This great order of Insects includes the "Beetles," which are characterised by their strong chitinous integument and the complete adaptation of the mouth-organs for biting, the mandibles being well developed. *The anterior wings are useless as organs of flight, and are hardened by chitine, so as to form protective cases* (*elytra*) *for the posterior wings, these being membranous, and being folded transversely and longitudinally in repose. The nervures of the hind-wings are few and distant, cross-veins being rarely developed. The inner margins of the elytra* (fig. 449) *are generally straight, and when in contact they form a longitudinal suture.*

As regards their distribution in time, the oldest types of the *Coleoptera*, recognised by Mr Scudder, belong to the *Curculionidæ* (Weevils), and appear in the Triassic rocks (*Curculionites prodromus*). The Jurassic rocks have yielded a number of types of this family also; while Heer describes other forms from the Cretaceous rocks of Greenland; and about one hundred species of Weevils, belonging mostly to existing genera, have been mentioned or described from the Tertiary rocks. The great existing families of the *Chrysomelidæ*, *Buprestidæ*, and *Carabidæ* (fig. 449, b) are also all represented by Triassic forms; and all have more or less numerous Jurassic and Tertiary representatives. Of the remaining

families of the *Coleoptera* the majority of the leading groups of the present day, such as the *Tenebrionidæ*, *Cerambycidæ*, *Scarabæidæ*, *Elateridæ*, *Staphylinidæ*, *Coccinellidæ*, *Hydrophilidæ*, and *Dytiscidæ* possess more or less numerous Jurassic representatives, and all

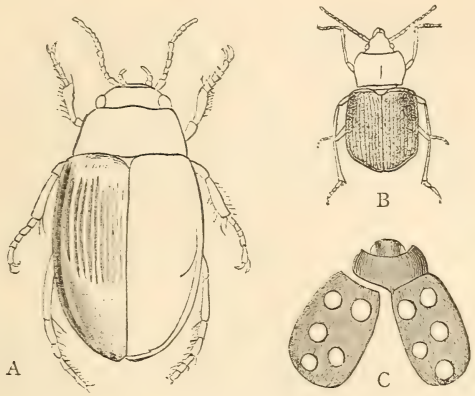

Fig. 449.—A, *Dytiscus Lavateri*, restored, from the Miocene deposits of Oeningen, of the natural size; B, *Thurmannia punctulata*, one of the *Carabidæ*, restored, and enlarged three times, from the Lias of Schambelen; C, *Coccinella decempunctata*, enlarged twice, from the Miocene deposits of Oeningen. (After Heer.)

occur under many specific forms in the Tertiary rocks. Many of the smaller families of Beetles are also known by fossil forms, but the order has attained its maximum development at the present day.

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CHAPTER XXXIII.

MOLLUSCOIDEA.

Polyzoa.

We may consider here, under the name of *Molluscoidea*, the two groups of animals which are known respectively as the *Polyzoa* and the *Brachiopoda*. These two groups, in many respects closely allied to one another, present affinities on the one hand to the Worms, and on the other hand to the *Mollusca*, with both of which they have been arranged by different systematists. In the present state of our knowledge, however, it seems best to consider these two groups separately, without referring them definitely to either of the two sub-kingdoms above mentioned. The Tunicates, which have also often been included amongst the Molluscoids, may likewise be in the meanwhile regarded as a separate division, which finds its most natural position between the *Mollusca* and the *Vertebrata*. It is not necessary, however, to further consider the Tunicates in this work, since the palæontological history of this group of animals is an almost absolute blank. No fossil remains of Tunicates have, in fact, been hitherto discovered except the minute spicules of a species of *Leptoclinum* in the Pliocene beds of St Erth. Many existing Tunicates, however, both simple and compound, are known to possess more or less numerous calcareous spicula in their tissues, and by the help of these it may ultimately be found possible to trace back the existence of these singular organisms to an earlier period of the earth's history.

The *Molluscoidea* may be briefly defined as unsegmented, simple or compound animals, with bilateral symmetry. The mouth is furnished with a crown of ciliated tentacles, or with spirally-rolled ciliated processes. The nervous system consists of a single ganglion, or of an œsophageal nerve-ring with more than one ganglion. A heart is absent or present. Under this head may be placed the two classes of the *Polyzoa* and the *Brachiopoda*.

Polyzoa.

Class I. Polyzoa (*Bryozoa*).—The members of this class are mostly *composite animals, each zoöid of which possesses, typically, a freely suspended alimentary canal, with mouth and anus, enclosed within a double-walled sac. The mouth is surrounded with a circle or crescent of hollow ciliated tentacles, and the nervous system consists of a single ganglion placed between the mouth and the anus.*

With the single exception of the genus *Loxosoma*, all the *Polyzoa* live in an associated form in colonies or "polyzoaria," which are sometimes foliaceous, sometimes branched and plant-like, sometimes laminar, sometimes encrusting, and very rarely are free. Each "polyzoarium" consists of an assemblage of distinct but similar zoöids arising by continuous gemmation from a single primordial individual. The entire colony—or its entire dermal system—is called the "polyzoarium" or "cœnœcium"; the separate zoöids are called "polypides"; and the little chambers in which each is contained are called the "cells," or "zoœcia."

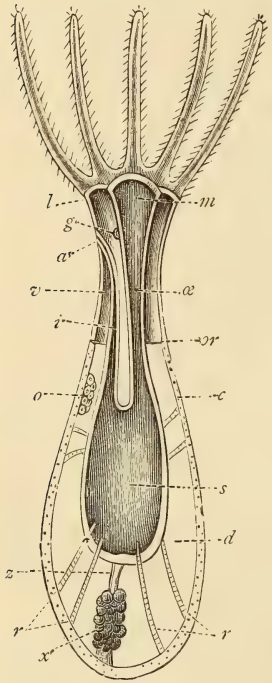


Fig. 450.—Diagram showing the structure of a single polypide of a Polyzoan (after Busk). *l*, Tentacles; *m*, Mouth; *g*, Nerve-ganglion; *œ*, Gullet; *s*, Stomach; *i*, Intestine; *a*, Anus; *o*, Ovary; *x*, Testis; *z*, Funiculus; *or*, Aperture of the zoœcium; *v*, Tentacular sheath; *d*, Perivisceral cavity; *r*, Retractor muscles; *c*, Ectocyst.

A typical polypide of a *Polyzoön* (fig. 450) consists of a membranous sac ("endocyst") the external surface of which, except at its anterior end, is generally hardened by an investing horny or calcified layer, which is known as the "ectocyst." Freely suspended in the perivisceral fluid filling the space enclosed within the endocyst is the alimentary canal, which consists of a mouth, gullet, stomach, intestine, and anus. The mouth (fig. 450, *m*) is placed anteriorly, and is surrounded by a crown of tubular, non-retractile tentacles, which are ciliated, and act as respiratory organs. In different types of the class, the tentacles are arranged in a circle or are disposed so as to form a horse-shoe or crescent. The alimentary canal is bent upon itself in such a way that the anus (fig. 450, *a*) comes to be placed near the mouth, being usually placed outside the tentacular circle

(in the "Ectoproctous" *Polyzoa*), but sometimes within it (in the "Entoproctous" *Polyzoa*). The alimentary canal is moored to the body-wall by muscular bands, those springing from the bottom of the cell serving to retract the polypide within its chamber, while the protrusion of the tentaculated anterior extremity is effected by muscular fasciculi which run in a circular manner in the wall of the cell.

Each polypide possesses a single nervous ganglion (fig. 450, *g*), which is placed upon one side of the gullet, between it and the anal aperture. The different polypides may also be connected together by a remarkable organic structure, which was at one time believed to be of a nervous nature, and was termed the "colonial nervous system," but which is now generally spoken of as the "endosarc." This singular connective system, by which the different polypides of the colony are organically united, commences as a peculiar cellular cord, the "funiculus" (fig. 450, *z*), which stretches from the base of the stomach to the bottom of the zoœcium, and upon which the testis is developed. At the point where the funiculus is fixed to the bottom of the cell, a perforation in the ectocyst exists, and filaments of the funiculus thus either pass into adjacent polypides, or become connected with a common branched fibre which runs through the stolons of the colony (as in *Bowerbankia*). In many cases the endosarcal cords give off branching fibres, and they have a general likeness to a nervous system. Histologically, however, the endosarc does not consist of nervous elements, and it may be regarded as a kind of cœnosarcal structure, which is largely connected with the production of the generative elements, and from which, possibly, the polypides are produced by gemmation.

The polypide of the *Polyzoa* is generally hermaphrodite, the ovary (fig. 450, *o*) being usually situated near the summit of the cell, attached to the inner surface of the endocyst, while the testis (*x*) is placed at the bottom of the cell, and is attached to the "funiculus." The generative elements are usually set free into the perigastric space, the ova being thus fecundated within the body-cavity of the parent polypide. The fertilised ova may pass into special dilatations of the cell ("ovicells"), or the embryos may be hatched within the perivisceral cavity of the parent.

The embryo is, to begin with, ciliated and freely locomotive, but ultimately fixes itself, and, except in *Loxosoma*, begins to produce a colony by means of budding. The new buds are usually produced from the dorsal wall of the polypide, or from its sides, or sometimes from its anterior extremity. Fission, so common among the Cœlenterates, has never been noticed to occur. The ultimate form of the polyzoary depends upon the precise method in which the new buds are developed. The separate polypides of the colony are ap-

parently always more or less clearly united with one another by an organic connection. In many cases this communication between the different polypides is effected by means of the structure which has been previously spoken of as the "endosarc." In other cases the walls of the cells are pierced by pores or traversed by tubuli, by means of which the perivisceral cavities of adjoining polypides are placed in communication. In other cases, again, there exists a common lamina, the extension of which precedes the production of new cells. Lastly, in the group of *Polyzoa* known as the *Ctenostomata*, there exists a common tube with which all the polypides of the colony are connected.

The structures in the *Polyzoa* with which the palæontologist is more especially concerned are those developed from the external

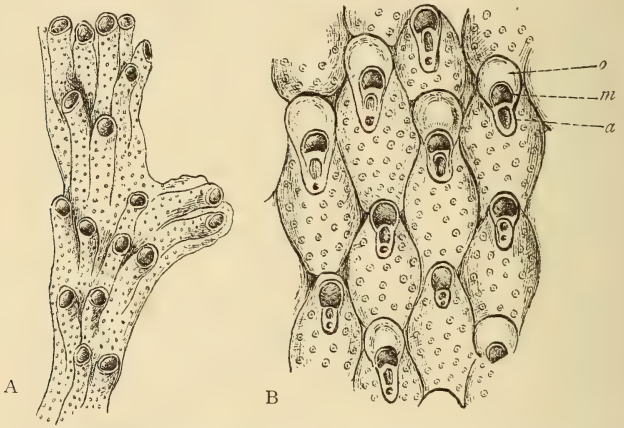


Fig. 451.—A, Fragment of *Stomatopora* (*Alecto*) *dilatans*, a recent Cyclostomatous Polyzoön, enlarged. B, A few cells of *Smittia Marionensis*, a recent Cheilostomatous Polyzoön, enlarged: *m*, Aperture of the cell; *a*, Avicularium; *o*, Ovicell. (After Busk.)

investing layer or "ectocyst," which form the skeleton of the colony, and which alone are capable of being preserved in the fossil condition. In rare cases among the existing *Polyzoa* the ectocyst may be absent, or may be gelatinous in consistence; but it is usually either purely chitinous or more or less extensively calcified. The ectocyst forms for each polypide of the colony a more or less complete "cell"; but the cell is invariably furnished at one point with an "aperture" or "mouth," whence the polypide can protrude its tentaculate head. In various forms, however, the anterior wall of the ectocyst may be imperfectly hardened, or may remain membranous. The form of the "cells" or "zoœcia" in the *Polyzoa* varies extremely in different groups, and important distinctions are

based upon this character. Thus, in the so-called "Cyclostomatous" Polyzoa the cells are tubular in form (fig. 451, A), and the aperture is terminal in position, and is approximately equal to the cell itself in diameter, while there is no special movable apparatus for its closure. On the other hand, in the so-called "Cheilostomatous" Polyzoa (fig. 451, B) the mouth of the cell is never quite terminal in position, but is always placed upon the front of the cell, generally close to the anterior end, while its diameter is less than that of the cell, and it is provided with a movable opercular valve.

The surface of the cell may be "either smooth and entire, spinous or granulous; perforated with minute pores, or cribriform with larger openings; reticulate or ribbed, &c.,—all of which conditions, with certain precautions, afford excellent diagnostic characters" (Busk). The margins of the mouth of the cell, also, may be "simple or thickened, unarmed or beset with erect 'marginal spines,' which again may be either rigid or articulated at the base, simple or branched."

Though the separate zoœcia of a Polyzoan colony are usually apparently quite separate and distinct from one another, except by continuity of their external investment, it has been shown that contiguous cells are commonly placed in direct connection with

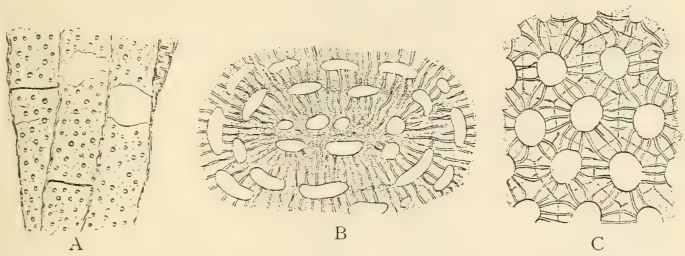


Fig. 452.—A, Longitudinal section of a few tubes of the recent *Tennysonia stellata*, enlarged, showing the porous walls of the cells; B, Central portion of a transverse section of a branch of *Cellepora ramulosa* (Recent), showing tubes connecting the cavities of adjoining cells, enlarged; C, Part of a tangential section of the polyzoary of *Domopora stellata* (Recent), enlarged to show the connecting-tubuli. (Original.)

one another by what have been called "communication-plates" or "rosette-plates." These are portions of the cell-wall pierced by one or more minute pores which transmit processes of the structure which has been previously described as the "endosarc." In many of the calcareous *Polyzoa* also, the walls of the cells are pierced by more or less numerous pores, which open into the cavity of the cell (fig. 451). In certain of the Cyclostomatous *Polyzoa*, as also in some Cheilostomatous forms, where the walls of the cells are of considerable relative thickness, these pores assume

the form of tubes, which place the perivisceral cavities of contiguous cells in direct communication, as is seen, for example, in such recent genera as *Cellepora* among the *Cheilostomata*, and *Domopora* and *Heteropora* among the *Cyclostomata*. These connecting-tubes (fig. 452) are usually wide and trumpet-shaped at the points where they open into the cavities of the cells, and are contracted in the middle portion of their course; and they, doubtless, are simply a further development of the simple pores seen in many other forms.

Again, in various of the Palæozoic *Polyzoa*, and particularly in the family of the *Fenestellidæ*, a portion of the polyzoary consists of dense calcareous tissue which exhibits under the microscope a finely punctated appearance. When sufficiently thin sections of this punctated layer are prepared, and examined with a sufficiently high magnifying power, the tissue is seen to be penetrated by innumerable exceedingly minute tubuli (fig. 453), which run at right angles to the surface of the polyzoary. Nothing certain has, however, been ascertained as to the nature and function of these tubuli. In some types, such as *Rhombopora* (*Ceriopora*) *interporosa*, of the Carboniferous rocks, the thickened walls of the cells near their mouths are penetrated by dark rod-like structures which run at right angles to the surface. These structures are of larger size than the tubuli of the Fenestellids, but they sometimes exhibit a clear central space, and it is probable that they are really of the nature of tubes.

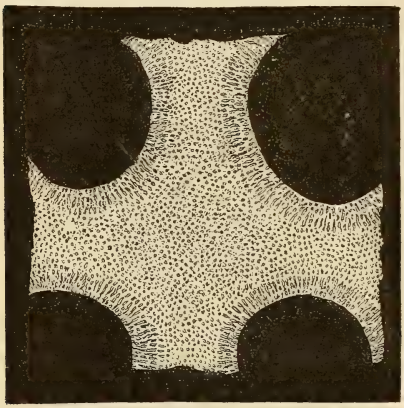


Fig. 453.—A portion of the punctated layer on the non-poriferous side of a Fenestellid (*Phyllopora* sp.), cut parallel with the surface and greatly enlarged. Devonian, Canada. (Original.)

In a great number of the recent *Polyzoa*, the polyzoarium is furnished with singular appendages, which are known as "avicularia" and "vibracula," and which are to be regarded as specially modified zoöids. The avicularia or "bird's-head processes" (fig. 454, B and C) differ a good deal in shape, but consist essentially of "a movable mandible and a cup furnished with a horny beak, with which the point of the mandible is capable of being brought into apposition" (Busk). In shape, the avicularia often closely resemble the head of a bird; and they are in many respects comparable with the "pedicellariæ" of the *Echinodermata*, keeping up a constant snapping movement which continues long

after the death of the general colony. In the "vibracula" (fig. 454, A), the place of the mandible of the avicularium is taken by a bristle, or seta, which is capable of extensive movement.

Owing to the minute size of the avicularia and vibracula and their readily perishable structure, it could hardly be expected that the fossil *Polyzoa* should exhibit similar organs except under the most favourable conditions of preservation; and as a matter of fact, these appendages have not hitherto been recognised except in a few instances. The former existence of avicularia may, however, be in many cases inferred by the presence of cicatrices or pore-like

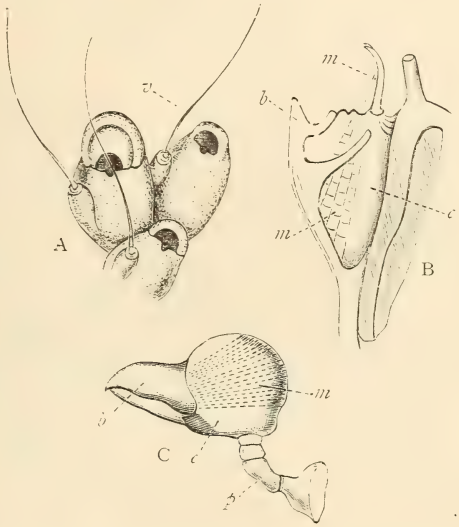


Fig. 454.—A, Three cells of *Mastigophora Hyndmanni*, showing vibracula (*v*)—the left-hand cell also shows an oœcium; B, Sessile avicularium of *Scrupocellaria scruposa;* and C, Pedunculate avicularium. *b*, Beak; *c*, Chamber of the avicularium; *m*, Muscles; *p*, Peduncle. All the figures are enlarged. (After Hincks and Busk.)

depressions on the surface of the cells. In some instances it can be shown, as, for example, in the recent *Retepora*, that the avicularia are really attached to thickened tubes which pass deep into the substance of the polyzoary, and which can therefore be readily recognised in thin sections (fig. 455, A). This observation is of considerable interest as affording a possible explanation of certain thickened tubular structures which are found in some of the Palæozoic *Polyzoa*. The structures in question have the form of tubes with thickened fibrous walls, embedded in the solid tissue of the polyzoary; and when cut across transversely in thin sections (fig. 455, B and C), they exhibit a minute central clear spot surrounded

by a dark margin. They were first recognised by Mr John Young as occurring in some of the *Fenestellidæ* (fig. 467), and they were compared by this observer with the "acanthopores" of the Monticuliporoids. They occur, however, in other Palæozoic *Polyzoa* beside the Lace-corals (as in *Coscinium* and in species of *Rhombopora*), and it may be conjectured that they are of the same nature as the small thick-walled tubes in the polyzoary of the existing *Retepora* (fig. 455, A), in which they support the avicularia.

In many of the *Polyzoa* the cells are furnished with special dilatations, which serve as marsupial pouches for the ova, and which are known as the "ovicells" or "oœcia." In general, these peculiar brood-pouches have the form of helmet-shaped or sac-like chambers springing from the anterior end of the cell (fig. 451, B, *o*), with

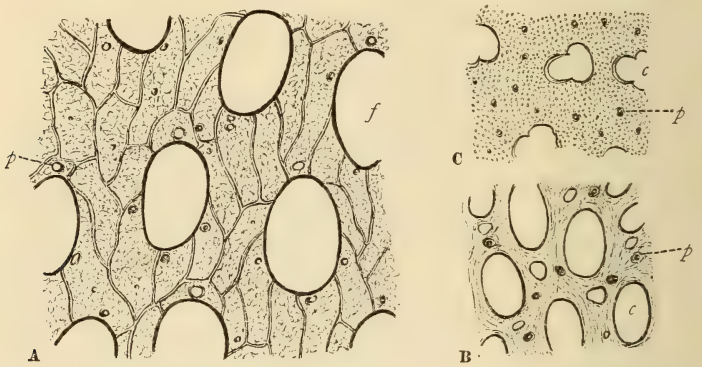


Fig. 455.—A, Tangential section of a recent species of *Retepora*, taken parallel to the non-poriferous surface of the polyzoary, enlarged, showing the thickened tubes (*p*) to which the avicularia were attached; B, Tangential section of *Rhombopora* (*Ceriopora*) *Hamiltonensis*, from the Devonian rocks of Canada, enlarged, showing thickened tubes (*p*); C, Tangential section of *Coscinium* (*Coscinotrypa*) *cribriforme*, from the Devonian rocks of Canada, enlarged, showing similar thickened tubes (*p*). *c*, Cavity of a cell; *f*, One of the "fenestræ" of *Retepora*. (Original.)

the cavity of which they communicate by an aperture or fissure in their hinder wall. Ovicells are not only found in the recent *Cheilostomata* generally, but occur also in numerous Secondary and Tertiary types. Mr Ulrich has likewise recognised in certain of the Fenestellids structures which appear to be of the nature of ovicells; but with this exception no traces of these organs have hitherto been detected in the Palæozoic *Polyzoa*.

In various of the Cyclostomatous *Polyzoa* the mouths of a greater or less number of the cells may be closed by a calcareous membrane, covering parts of the surface more or less completely. In other cases (as in *Mesenteripora* and sometimes in the Palæozoic *Polypora*), individual cells may have their mouths closed by a calcareous lid, which may exhibit a minute central perforation, or, in

other cases, a projecting tubule. Mr Waters has further shown that in the *Cyclostomata* it is not uncommon for a calcareous plate to be developed at the point where the zoœcial tube rises free from the polyzoarium; while in other cases, two of these "closing-plates" are developed close together. Probably of a similar nature to the "closing-plates" just mentioned are the transverse calcareous partitions which are developed in the tubes of various Cyclostomatous *Polyzoa*, both recent and fossil, and which have been spoken of as "tabulæ," from their similarity to the structures known by this name in many Corals. These so-called "tabulæ" differ from the "closing-plates" described by Mr Waters in being developed in the deeper

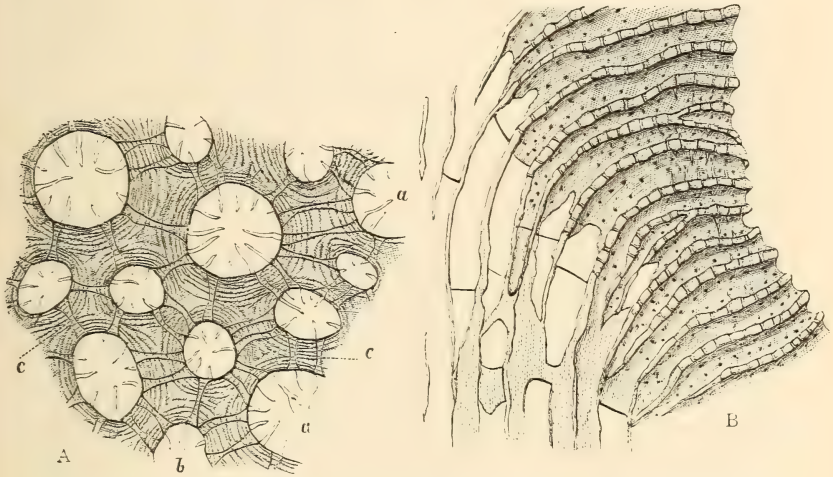


Fig. 456.—Minute structure of the recent *Heteropora pelliculata*, Waters (= *H. neozelanica*, Busk). A, Tangential section of the polyzoary, enlarged about fifty times, showing the proper zoœcia (*a*, *a*) and interstitial tubes (*b*) connected by numerous minute tubules (*c*). The cells are furnished with numerous radiating spines or "rays." B, Part of a longitudinal section, enlarged about twenty times, showing connecting-pores, "rays," and delicate transverse partitions or "tabulæ." (Original.)

as well as in the more superficial portions of the colony, and they are sometimes present in considerable numbers. They occur in various genera, as, for example, in *Heteropora* (fig. 456, B), *Alveolaria*, *Fascicularia*, *Lichenopora*, &c.; and they are probably connected with the periodic death and renovation of the polypides which is known to occur in many recent *Polyzoa*.

In certain of the *Polyzoa*, finally, the cells are furnished with delicate, radially disposed spines, which present a superficial resemblance to the "septa" of such corals as *Favosites* and certain of the *Heliolitidæ*, and which may be spoken of as "rays." These curious structures (fig. 456, A) have the form of minute calcareous

spines which are directed into the interior of the cell-cavity, their free ends being sometimes globular or button-like. They have been recognised by the present writer in the recent *Heteropora pelliculata* and in some species of *Lichenopora* (*Discoporella*); while Mr Waters has detected them in *Entalophora intricaria*, and in species of *Tubulipora* and *Lichenopora;* and apparently identical structures have been shown by Mr John Young to exist in certain of the *Fenestellidæ*. So far as known, these "rays" are confined to certain of the Cyclostomatous *Polyzoa*, and their precise morphological significance has not as yet been determined. According to a curious observation of Mr Waters, the zoœcia of *Lichenopora grignonensis* not only possess "rays" in their interior, but are also furnished with similar spines projecting from portions of the *external* surface.

As regards their *classification*, the *Polyzoa* may be divided into the three primary sections of the *Ectoprocta*, *Entoprocta*, and *Aspidophora*, of which the last two require no further characterisation here, as they are not known to possess any fossil representatives. The division of the *Ectoprocta*, on the other hand, includes the great majority of the living *Polyzoa* and the whole of the fossil forms, though the essential feature of the division is the position of the anal opening outside the tentacular circle,—a character which, necessarily, can only be positively determined in living examples. The *Ectoprocta* may be divided into the two orders of the *Phylactolæmata* and *Gymnolæmata*, the former characterised by the almost universal feature that the tentacular crown is horse-shoe-shaped, and by the possession of a peculiar valve-like organ ("epistome") arching over the mouth; while the tentacular crown in the latter is circular and there is no epistome. The Phylactolæmatous *Polyzoa* are confined to fresh waters, and they need not be considered here further, as no fossil examples of the order have ever been detected. The order of the *Gymnolæmata*, on the other hand, is of great importance, as comprising the vast majority of the existing marine *Polyzoa* and all the known fossil forms. The order may be divided into the three sub-orders of the *Cyclostomata*, the *Cheilostomata*, and the *Ctenostomata*, the first two characterised by the form of the cell and the absence or presence of an opercular valve to the cell-aperture, while the last is distinguished by the fact that the cells arise from a common tube, their mouths being terminal and furnished with a setose fringe for their closure.

As regards their *distribution in time*, the earliest known forms of the *Polyzoa* are found in the Ordovician rocks, and all the later Palæozoic formations abound in Polyzoan remains. Even in the Ordovician rocks the *Gymnolæmata* are represented by numerous and very widely different types, and the primitive forms of the class must have existed in Cambrian or in even earlier periods. The

Palæozoic *Polyzoa* appear to be for the most part referable to the Cyclostomatous division of the *Gymnolæmata*, and no unequivocal examples of the *Cheilostomata* have been hitherto recognised in any Palæozoic formation. The form described by the present author from the Ordovician rocks as *Hippothoa? inflata* is referable to *Stomatopora* (as this genus is usually understood), and in that case is Cyclostomatous, as also is the *Hippothoa devonica* of Œhlert. It is, however, possible that the Palæozoic genus *Paleschara*, of Hall, is really Cheilostomatous. While the Palæozoic *Polyzoa*, therefore, must in the meanwhile be referred in a general way to the *Cyclostomata*, it has to be borne in mind that many of them exhibit very peculiar characters, and that certain forms are apparently transitional between the *Cyclostomata* and the *Cheilostomata*. It is, in fact, not improbable that fuller investigation of the characters and structure of the Palæozoic *Polyzoa* will render it necessary to recast the classification of the *Gymnolæmata;* and steps in this direction have already been taken by Mr Ulrich. It does not seem possible, however, to accomplish this satisfactorily at present, since we are not only still imperfectly acquainted with the minute structure of many Palæozoic *Polyzoa*, but there are various Palæozoic organisms, the precise place of which in the zoological series has not yet been ascertained with certainty. This is notably the case with the great Palæozoic group of the Monticuliporoids, which, for reasons previously given (see p. 352), have been here placed provisionally beside the Cœlenterates, while they are regarded by Lindström, Ulrich, and other authorities as belonging to the *Polyzoa*. It is also not impossible that we may have in the Palæozoic rocks representatives of other groups of the existing *Polyzoa* than the *Cyclostomata* and *Cheilostomata*. Thus, the singular genus *Ascodictyon*, of the Silurian, Devonian, and Carboniferous rocks, may possibly be, as suggested by Mr Vine, a representative of the *Ctenostomata*, or may even be referable to the section of the Entoproctous *Polyzoa*.

The earlier Secondary deposits (Trias and Lias) have hitherto yielded very few remains of *Polyzoa;* but numerous forms of this class are known in the later Jurassic and in the Cretaceous rocks, the Upper Chalk, in particular, being extraordinarily rich in the remains of these organisms. In the earlier part of the Secondary period, by far the larger number of the known *Polyzoa* are still referable to the *Cyclostomata*, but in the later portion of the Cretaceous period the *Cheilostomata* are likewise largely represented. In the Tertiary rocks, again, not only are the remains of *Polyzoa* abundant, but the majority of the forms represented are now referable to the *Cheilostomata*, the Cyclostomatous types undergoing a decided reduction. All the great divisions of the Tertiary rocks have yielded

more or less numerous *Polyzoa* (fig. 457); but the Upper Oligocene of Germany, the Miocene deposits of France, Austria, Switzerland,

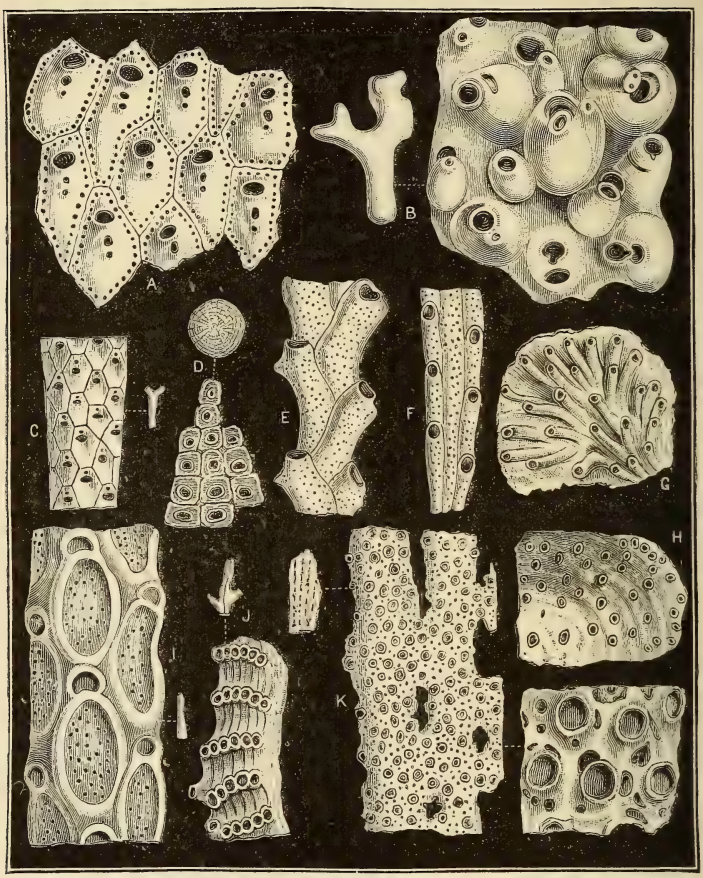


Fig. 457.—Types of Tertiary Polyzoa. A, A few cells of *Microporella violacea* (Pliocene and Recent), magnified; B, *Cellepora coronopus*, of the natural size, and a portion of the surface enlarged (Pliocene); C, A small piece of *Cellaria* (*Salicornaria*) *crassa*, of the natural size and enlarged (Pliocene); D, *Lunulites quadrata*, of the natural size, and a small portion of the upper surface enlarged (Tertiary); E, A fragment of *Scrupocellaria elliptica*, viewed from behind, enlarged (Tertiary); F, A small piece of *Crisia denticulata* (Tertiary), enlarged; G, A fragment of *Tubulipora flabellaris* (Tertiary), enlarged; H, A fragment of *Diastopora simplex*, enlarged (Tertiary); I, A piece of *Vincularia Haidingeri*, natural size and enlarged (Tertiary); J, *Idmonea fenestrata*, natural size and enlarged (Tertiary); K, *Hornera reteporacea*, natural size and enlarged (Tertiary). (After Busk and Reuss.)

and Italy, and the Pliocene beds ("Coralline Crag") of Britain, have proved particularly rich in the remains of these organisms.

In the following general account of the characters and chief groups

of the fossil *Polyzoa*, no attempt will be made to give a complete review of the different families. Not only is the classification of the fossil *Polyzoa* in an admittedly unsatisfactory state, but the characters of many of the fossil types cannot be rendered intelligible without the free use of illustrations, even where these are thoroughly understood; while there are many types the structure of which is at present only imperfectly known. Nothing further will therefore be attempted here than to shortly characterise some of the more important and more widely distributed groups, and to indicate the chief forms of these and their general geological range; all the fossil types here referred to being provisionally distributed between the *Cyclostomata* and the *Cheilostomata*.

Sub-Order I. Cyclostomata.

This sub-order, as has been previously seen, includes Gymnolæmatous *Polyzoa*, in which the cells are more or less tubular, the cell-aperture being terminal, usually of the same diameter as the tube itself, and not provided with a movable operculum for its closure. In a large number of the *Cyclostomata*, the tubes (fig. 451, A) are free for a larger or smaller portion of their length, so that the surface of the colony is partly formed by the lateral walls of the zoœcia; while in other types (fig. 456, B) the tubes are in contact throughout their entire length, the cells thus opening at right angles to the axis or surface of the colony, and the whole exterior being thus occupied by the cell-apertures. This difference probably expresses a genuine structural distinction, and upon it Mr Waters has proposed to divide the *Cyclostomata* into the two divisions of the *Parallelata*, with partially free tubes, and the *Rectangulata*, with the tubes in contact throughout.

In most of the *Cyclostomata* the calcareous walls of the cells are pierced by smaller or larger pores, but in some cases the walls appear to be completely imperforate. In many forms all the cells are similar to one another, but in others (*e.g.*, in *Heteropora*) the colony consists of two sets of tubes, which are similar in internal structure, but differ in point of size. In other forms referred to this sub-order an interstitial vesicular tissue appears to be developed between the proper zoœcia. "Ovicells" are developed in certain of the *Cyclostomata*, but they have not been observed in others, and they do not play such a conspicuous part as they do in the *Cheilostomata*. In various forms of the *Cyclostomata*, finally, radiating spines or "rays" are developed in the cells, while the structures previously alluded to as "closing-plates" and "tabulæ" are not uncommonly present.

The *Cyclostomata* are the most ancient group of the *Polyzoa*,

being represented by numerous forms in all the great geological formations from the Ordovician onwards. With a few possible exceptions, as already noted, the whole of the Palæozoic *Polyzoa* may be provisionally referred to the *Cyclostomata;* but while some of even the oldest forms belong to quite normal groups of this suborder, others differ widely from the regular type, and will probably be ultimately referred elsewhere. Leaving these last out of consideration, the *Cyclostomata* may be said to attain their maximum development in the Jurassic and Cretaceous rocks, a decided diminution in their numbers taking place in the Tertiary period.

Taking the normal groups of the *Cyclostomata* first, and leaving out of sight certain comparatively unimportant types, the family of the *Crisiidæ* comprises a small number of dendroid forms, in which the polyzoary consists of calcareous segments united by corneous joints, the tubular zoœcia being either uniserial or biserial (fig. 457, F). The type of this family is *Crisia* itself, which is represented by numerous Tertiary and recent species.

The family of the *Tubuliporidæ* (*Stomatoporidæ*) comprises forms in which the polyzoary is usually creeping and wholly adherent by its under surface, or partially free and erect. The tubular zoœcia may be disposed uniserially, or biserially, or irregularly grouped, their upper ends being more or less extensively free. The ovicells are represented by "an inflation of the zoarium at certain points, or a modified cell" (Hincks).

In the genus *Tubulipora* itself the colony is more or less extensively attached by its base (fig. 457, G), and the tubular zoœcia are free for a great part of their length and radiate from an excentric point. The species of this genus range from the Cretaceous rocks to the present day. The forms included under the head of *Stomatopora* (*Alecto*) differ considerably in their characters. In one group of forms comprised under this generic name the colony is completely adherent to foreign bodies, and the tubular cells are more or less extensively immersed, being free close to their mouths only; so that a more or less strap-shaped, often branched frond is produced (figs. 451, A, and 459, B and C), the walls of the zoœcia being at the same time porous, and usually either biserial or multiserial. In some forms (*Proboscina*), the polyzoary has the above characters, but is partially free and erect. Forms of the type here indicated are found in rocks as ancient as the Ordovician, while numerous species still exist. On the other hand, there have been included in *Stomatopora* various forms in which the polyzoary consists of a creeping adherent network, formed of uniserial or sometimes alternatingly biserial cells, which spring directly from each other, each new tube being produced from the anterior end of the lower surface of the preceding cell (figs. 458 and 459, D). The tubes are thick-walled and destitute of pores, and the colony often closely resembles an *Aulopora* in form. Indeed, the only essential distinction between such colonies and *Aulopora* is to be found in the fact, that in the typical species of the latter there appears to be a creeping basal network from which the tubes are sent up at intervals, instead of springing directly from one another; but it is not clear

how far even this distinction can be relied upon. Forms of this second type occur from the Ordovician rocks onwards. It would seem that these two groups of *Stomatoporæ* should be generically separated from one another, as the differences above pointed out are of substantial import-

Fig. 458.—A specimen of *Stomatopora dichotoma*, from the Great Oolite, of the natural size. (After Zittel.)

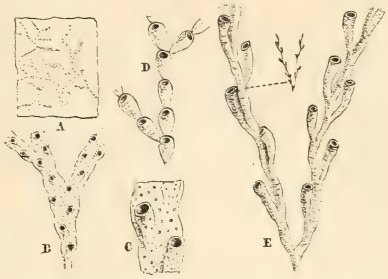


Fig. 459.—A, A fragment of shell with *Stomatopora auloporoides* and *S. inflata* growing on it, of the natural size, from the Cincinnati group (Ordovician) of America; B, *Stomatopora auloporoides*, enlarged; C, Part of the same, enlarged still further; D, *Stomatopora inflata*, enlarged; E, Fragment of *Hederella Canadensis*, from the Devonian rocks of Canada, of the natural size and enlarged. (Original.)

ance. It would also seem certain that the Silurian and Devonian genera *Reptaria* and *Hederella* (fig. 459, E), sometimes placed among the Corals, should be referred to this family. In these doubtfully distinct genera the colony is branched and adherent to foreign bodies by its lower surface, the branches consisting of long, narrow tubular cells, which spring in an alternating manner from one another, each branch being thus biserial.

Allied to the preceding is the family of the *Diastoporidæ*, in which the polyzoary is usually encrusting and discoid or fan-shaped, though sometimes foliaceous and erect. The tubular cells are in

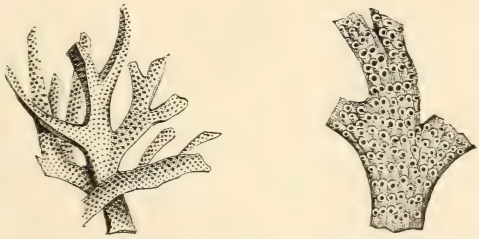


Fig. 460.—*Mesenteripora* (*Bidiastopora*) *cervicornis*, natural size and enlarged. Jurassic.

great part immersed, their ends only being usually free, and the peripheral part of the colony may be formed of small, angular "germinal" cells. The species of *Diastopora*, in a restricted sense, form small crusts upon foreign bodies, and range from the Jurassic to the present day. Allied types appear in the Silurian rocks, and

have been referred by Mr Vine to the genus *Diastoporella*. The foliaceous and erect forms of *Diastopora* are sometimes included under the separate generic name of *Mesenteripora*, or, if consisting of two layers of cells placed back to back, of *Bidiastopora* (fig. 460).

Berenicea comprises forms which hardly appear to be separable from *Diastopora;* but the typical forms placed under this head consist of crusts of superimposed cells. The genus has been quoted from the Ordovician rocks, and there are numerous undoubted Secondary, Tertiary, and Recent species.

Also related to the *Tubuliporidæ* is the family of the *Entalophoridæ*, in which the polyzoary is erect and free, rising from an expanded adherent base, and formed of long tubular cells which usually open all round the stems. The genus *Entalophora* (*Pustulopora*) itself ranges from the Jurassic to the present day, and has the cells open-

Fig. 461.—*Entalophora* (*Pustulopora*) *cellarioides*, of the natural size and enlarged. Jurassic.

ing irregularly on all sides of the branches. The name of *Spiropora* is usually given to forms essentially similar to the preceding, but having the cells so disposed that the cell-mouths form simple circles or spirals round the stems. Species of *Spiropora* appear as early as the Silurian period, and numerous Secondary and Tertiary types are known, while the genus still survives.

In the family of the *Idmoneidæ*, the polyzoary is erect, and almost always more or less branched, the branches being usually round, and sometimes anastomosing with one another. The tubular cells open on one side only of the polyzoary. In the genus *Idmonea* itself (fig. 457, J) the cells are disposed in transverse or oblique rows on each side of the front faces of the branches, which are divided mesially by an angulation or longitudinal keel. The genus ranges from the Chalk to the present day. In the genus *Hornera* (fig. 457, K), again, the polyzoary is branched and sometimes reticulated, the cells opening on one side of the branches only, their mouths being commonly placed in somewhat rhomboidal spaces marked out by wavy anastomosing ridges. Interstitial pores occur between

the cell-mouths, and may be developed on the non-celluliferous dorsal surface. The earliest undoubted species of *Hornera* occur in the Cretaceous rocks, and there are numerous Tertiary and recent types.

The family of the *Lichenoporidæ* comprises discoid polyzoaria, which sometimes in process of growth become confluent, or may even become massive, the colony being fixed by a broad adherent base or by a narrow peduncle. The zoœcia are tubular and erect, and are in complete contact throughout, or are free towards their extremities. The walls of the zoœcia may be porous or imperforate, and the proper zoœcia may be separated by intermediate cancellated or porous spaces.

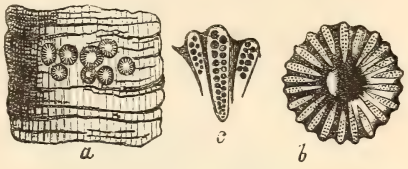


Fig. 462.—*Botryllopora socialis*, from the Devonian rocks of Canada. *a*, A small colony attached to a coral, of the natural size; *b*, A single disc of the same, enlarged; *c*, A small portion of the same, enlarged still further. (Original.)

The most ancient type of the *Lichenoporidæ* appears to be the genus *Botryllopora* of the Devonian rocks (Hamilton formation) of Canada and the United States. In this genus (fig. 462) the polyzoary consists of separate or confluent discs, which are attached by the whole of the under surface to foreign bodies. Each disc shows a series of elevated ridges or ribs, which radiate from a central area and are separated by intervening furrows. The ribs carry the apertures of the tubular zoœcia, and the spaces between them appear, in well-preserved specimens, to be minutely porous. The genus *Lichenopora* (*Discoporella*) comprises forms in which the polyzoary has the form of a simple disc or of numerous confluent discs, each disc being composed of tubular cells, which are arranged in lines radiating from a central space, and separated by intervening intervals. The zoœcia are free towards their mouths, and project above the general surface; and the spaces between them, as well as the central area, are occupied by smaller interstitial tubes or "cancelli." In some forms, both the proper zoœcia and the "cancelli" are provided with delicate capitate "rays." In many structural features *Lichenopora* closely approaches *Heteropora*, but the zoœcia of the latter are in contact throughout, and are not free towards their extremities. The forms with confluent discs are sometimes separated to constitute the separate genus *Radiopora*. The earliest types of *Lichenopora* (if considered as embracing *Radiopora*) appear in the Trias; while the genus has Jurassic, Cretaceous, and Tertiary representatives, and still survives at the present day. In the genus *Domopora* (*Defrancia*) the polyzoary is discoidal or massive, simple or lobed, attached by the whole base or by a stalk, or sometimes free. The zoœcia are "disposed in radiating lines, consisting of one or more series, on the free extremity of the stem or lobes" (Hincks), and their mouths do not project above the general surface. The walls of the zoœcia are penetrated by numerous delicate tubuli. This genus should perhaps be removed to the family of the *Heteroporidæ*. The species of *Domopora* appear first in the Jurassic, and are abundant in the Chalk, while Tertiary and living forms are also known.

The singular genus *Alveolaria* (fig. 463) may likewise be associated with the *Lichenoporidæ*—the only described species being the *A. semiovata* of the Red Crag (Pliocene) of Britain. In this remarkable form the polyzoary is massive and globose, consisting of numerous mushroom-shaped discs or cups, which are arranged in radiating and diverging lines, the cups of each vertical series springing directly from one another (fig. 463, C); and the different groups being so disposed that they form a series of thick concentric layers. Each concentric stratum is thus made up of a number of discs which are firmly united by their edges, but are free towards their bases; and each disc is enclosed in a strong calcareous membrane, the upper surface alone being free, and ex-

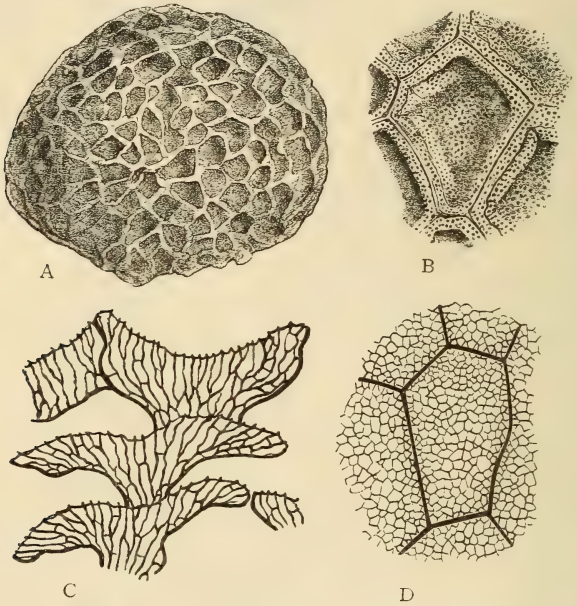


Fig. 463.—*Alveolaria semiovata*, from the Red Crag (Pliocene) of Britain. A, A specimen of the natural size; B, A portion of the surface enlarged; C, Part of a vertical section enlarged; D, Part of a tangential section enlarged. (Original.)

hibiting the apertures of the cells. The laterally-united discs are polygonal, and the surface (fig. 463, A and B) thus shows a number of polygonal cups bounded by strongly elevated ridges, each of which, in turn, exhibits a raised median line corresponding with the free edge of the epithecal membrane. For the same reason, tangential sections (fig. 463, D) show that the tubes are divided into polygonal groups, each of which is bounded by a strong external wall. The tubes themselves are in close contact throughout, their mouths not projecting above the general surface. The walls of the tubes are apparently completely imperforate; but "closing-plates" or "tabulæ" are often developed.

The family of the *Frondiporidæ* (*Theonoidæ*) includes forms in which the polyzoary is composed of long contiguous tubes, the

mouths of which are commonly disposed in groups of different size and form, separated by porous or imperforate interspaces. The genera *Frondipora* and *Fasciculipora* (*Fungella*) are both represented by species which range from the Chalk to the present day, and there are several other genera which are found in the Cretaceous or Tertiary rocks. Of the Tertiary forms the most interesting is the genus *Fascicularia* (*Mæandropora*), which is exceedingly abundant in the Red Crag (Pliocene) of Britain. In this genus (fig. 464) the

Fig. 464.—*Fascicularia* (*Mæandropora*) *cerebriformis*. Tertiary.

polyzoary is more or less massive, generally globose, and often of large size, composed of long calcareous tubes arranged in bundles, the tubes of each bundle being in contact, and the bundles being enclosed laterally in a calcareous membrane. The bundles diverge from the base of the colony, and may be connected by horizontal and concentric plates, or may be confluent by their sides and thus give rise to vertical convoluted laminæ. The tubes are destitute of "rays," but exhibit horizontal "tabulæ," and have minutely porous walls. In the common *Fascicularia aurantium* of the Red Crag the tubes open on the surface in sinuous anastomosing ridges, while in the allied *F. tubipora*, of the same formation, they open on rounded eminences.

The family of the *Heteroporidæ* is in some important respects related to that of the *Lichenoporidæ*, and comprises the genera *Heteropora* and *Heteroporella*. The polyzoary in this family may be erect and branched, or may be encrusting; and is composed of tubular zoœcia which are interspersed among similarly tubular but somewhat smaller "cancelli," all the tubes being in close contact throughout, and the mouths of the zoœcia not projecting above the general surface. The walls of the zoœcia and interstitial tubes or cancelli are penetrated by minute tubules, which place contiguous cells in communication (fig. 456); and in some species at any rate, delicate radiating spines ("rays") are developed. There is also generally a larger or smaller number of "closing-plates" or "tabulæ," which are principally developed in the deeper parts of the colony. In the genus *Heteropora* itself, the colony is erect and branched, the tubes being vertical in the centre of the branches, but bending out-

wards to reach the surface, their walls being considerably thickened in the outer part of their course (fig. 456, B). The earliest forms of *Heteropora* appear in the Jurassic rocks, and the genus has survived to the present day. The forms included by Busk in *Heteroporella* are Cretaceous and Tertiary, and the polyzoary is said to differ from that of *Heteropora* in being discoid and encrusting.

The family of the *Fenestellidæ* or "Lace-corals" constitutes one of the largest and most important groups of the Palæozoic *Polyzoa*, no Secondary or Tertiary types belonging to this family having been

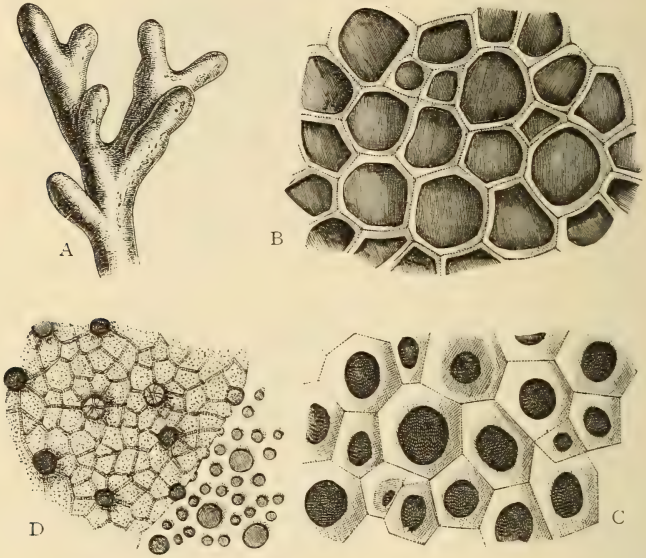


Fig. 465.—*Heteropora pelliculata*, Waters (=*H. neozelanica*, Busk), a recent species of *Heteropora*. A, A fragment of the polyzoary of the natural size; B and C, Portions of the surface of different specimens, enlarged, showing the apertures of the zoœcia and cancelli; D, A portion of the surface of another specimen in which the mouths of the cancelli and some of the zoœcia are in places covered by a calcareous pellicle, enlarged. (After Busk, Waters, and the Author.)

hitherto recognised. In all the members of this family the polyzoary is reticulated, generally fan-shaped or funnel-shaped, and composed of rigid, calcareous, parallel or slightly diverging branches, which may be united by cross-bars or "dissepiments," or may be sinuous and may unite regularly by anastomosis; the frond coming in both cases to be perforated by symmetrically disposed, sub-quadrate or oval spaces or "fenestrules" (figs. 466 and 467). The zoœcia have the form of short, utricular tubes, arranged in two or more series on one side only of the branches, the reverse side being non-poriferous, and being commonly finely striated. When true "dissepiments" are present, they are non-poriferous. The mouths of the zoœcia are

more or less circular, and are often provided with a projecting lip or "peristome."

The minute structure of the polyzoary in the *Fenestellidæ* appears to be very uniform. The cells themselves are formed of a layer of

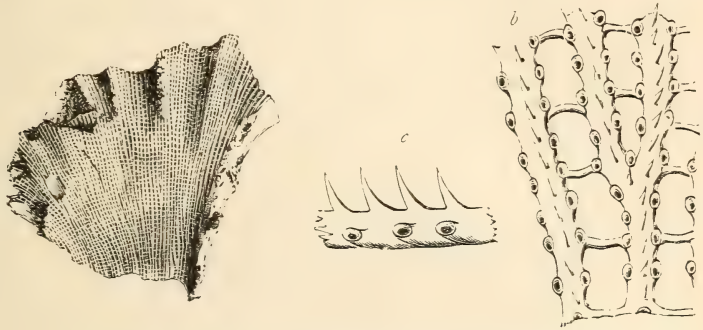


Fig. 466.—*Fenestella Lyelli*. *a*, Natural size; *b*, Portion enlarged; *c*, Cells and spines in profile. From the Carboniferous rocks of Canada. (After Dawson.)

perfectly homogeneous compact calcite, which is strengthened by a basal striated membrane; while the reverse or non-poriferous side of the polyzoary is composed of a thick stratum of calcareous tissue

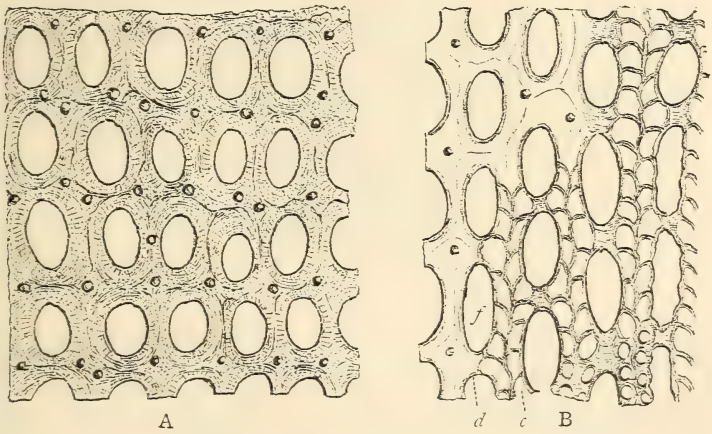


Fig. 467.—Minute structure of *Fenestella tuberculocarinata*, from the Carboniferous rocks of Scotland. A, Section taken parallel to the non-poriferous surface, showing thickened tubes (for the support of "avicularia"?), enlarged. B, Section parallel to the celluliferous surface of the polyzoary, showing the biserial cells (*c*): *d*, Dissepiments; *f*, Fenestrules. (Original.)

traversed by exceedingly minute tubuli, the direction of which is perpendicular to the surface, and which communicate to thin sections of this region of the skeleton an exceedingly characteristic

appearance (fig. 453). In some cases, as previously noted, the dorsal or non-poriferous side is traversed by remote, thick-walled, and comparatively large tubes (fig. 467, A), which may project above the surface of the polyzoary, and which may, perhaps, have served for the support of processes similar to the "avicularia" of the recent *Polyzoa*. In certain forms of the *Fenestellidæ* (species of *Fenestella* and *Polypora*), it has been shown by Mr John Young that the polyzoary was furnished on its margins or external surface with certain remarkable appendages, which were originally described by Professor Martin Duncan and Mr Jenkins under the name of *Palæocoryne*,

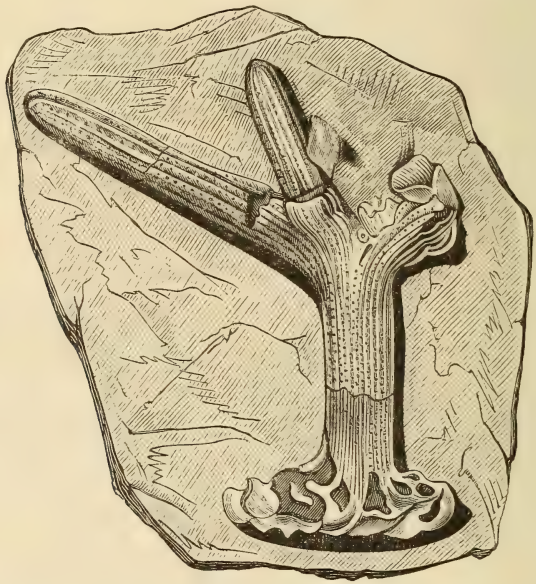


Fig. 468.—Branched appendage of a Fenestellid (the *Palæocoryne radiatum* of Duncan and Jenkins), enlarged fifteen diameters. (After Martin Duncan and H. M. Jenkins.)

and which were regarded by these observers as belonging to the *Hydrozoa*. The appendages in question (fig. 468) are of small size, and have the form of short, robust, calcareous stems, which spring from an expanded base, and are usually marked with longitudinal flutings or superficial granulations, while the free extremity generally terminates in a whorl of similarly fluted and ornamented cylindrical processes. In some cases, as shown by Mr John Young, the terminal processes may be curved or hooked, or they may be even united by lateral cross-bars. The observations of Mr Young prove conclusively that the structures described under the name of *Palæocoryne* truly form parts of the Polyzoan to which they are

attached, since thin sections prove the absolute continuity of the substance of the two; while the processes themselves consist, as does the polyzoary from which they spring, of an external finely-tubulated layer and an internal homogeneous stratum. The nature and use of these singular appendages cannot at present be more than guessed at.

As regards the chief types of the *Fenestellidæ*, the genus *Fenestella* itself ranges from the Silurian to the Permian inclusive, and comprises a large number of species, the greater part of which belong to the Devonian and Carboniferous rocks. In this genus (figs. 467, 468, and 469, C and

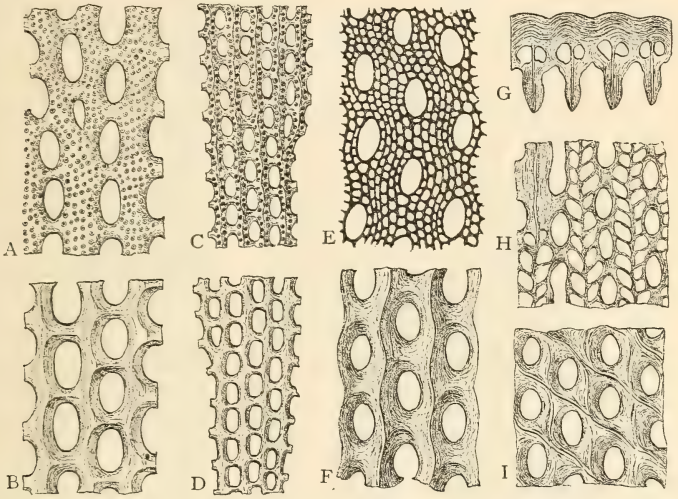


Fig. 469.—A, Poriferous side of *Polypora rigida* (Devonian); B, Non-poriferous side of the same; C and D, Poriferous and non-poriferous sides of *Fenestella biseriata* (Devonian); E, Section of *Phyllopora* sp. (Devonian), showing the anastomosing branches and the form and arrangement of the cells; F, Non-poriferous side of the same; G, Transverse and vertical section of *Carinopora Hindei* (Devonian), showing the greatly developed keels, with the biserial cells at their bases; H, Section of the same parallel with the poriferous face; I, Part of the non-poriferous side of the same. All the figures are enlarged. (Figs, A—D are after Hall; E—I are original.)

D), the polyzoary is fan-shaped or infundibuliform, the cells being developed on one side only, this being generally, if not always, the *inner* side of the colony. The branches are straight, and are connected at short intervals by regularly placed, non-poriferous cross-bars, or "dissepiments." The zoœcia are always biserial, the two rows of each branch being separated by a median ridge or keel. In its general structure the Devonian genus *Carinopora* (fig. 469, G—I) resembles *Fenestella*, the polyzoary being funnel-shaped, with the cells opening on the *inside*, and each branch having a double row of cells separated by a median keel. In this genus, however, the keels on the branches are enormously developed, and the external aspect of the polyzoary resembles that of *Phyllopora*. The genus *Semicoscinium*, also from the Devonian rocks, is considered by Ulrich as identical with *Carinopora*, but in this case the zoœcia open

on the *outside* of the funnel-shaped polyzoary. The remarkable Devonian genus *Unitrypa*, again, resembles the two preceding types in general structure; but the projecting keels which separate the two rows of cells on each branch are widened at their summits, and are connected with one another by thin lateral processes placed at variable distances. In the Carboniferous genus *Ptilopora* (fig. 470) are included forms which agree in essential structure with *Fenestella*, but differ in the feather-like form of the frond, the polyzoary having a central stem which gives off lateral branches in a pinnate manner, these latter being connected by dissepiments separated by oval fenestrules. The genus *Archimedes* (*Archimedipora*) is another remarkable Carboniferous type, in which the general structure is like that of *Fenestella*, but the reticulate polyzoary is wound in an obliquely spiral manner round a central screw-like axis (fig. 471, *c*). The genus *Helicopora* has a similarly spiral zoarium, but there

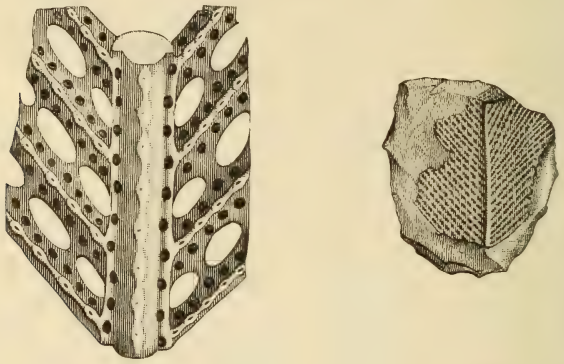


Fig. 470.—*Ptilopora pluma*; the right-hand figure of the natural size, the left-hand figure enlarged. Carboniferous.

is no central axis developed. *Lyropora*, from the Carboniferous rocks of North America, resembles *Fenestella* in general features; but the net-like polyzoary is bounded by solid lateral supports, which spring, like the two branches of the letter U, from a small base of attachment. Lastly, the genus *Fenestralia*, likewise from the Carboniferous rocks of North America, differs from *Fenestella* principally in the fact that there are *two* rows of cells on each side of the median keel in each branch.

The Carboniferous genus *Actinostoma* resembles *Fenestella* in having a fenestrated polyzoary which is poriferous on one side only; but the branches are not keeled, the cell-mouths are furnished with radiating teeth or "rays," and the zoœcia have a second supplementary pore close to the proper aperture. The widely distributed genus *Polypora* (fig. 469, A and B, and fig. 471, *a*) agrees with *Fenestella* in general structure, but the branches are not keeled, and there are from three to six rows of cells to each branch. As in *Fenestella*, however, the branches are connected by solid, non-poriferous "dissepiments." On the other hand, in the genus *Phyllopora* (the *Retepora* of many authors) the branches which compose the funnel-shaped polyzoary are not joined by dissepiments, but are sinuous, and anastomose with one another at short and regular intervals, so as to give rise to a symmetrically disposed system of "fenestrules" (fig. 469, E and F). The zoœcia are placed on the inner side of the frond,

each branch having from two to five rows of cells. The species of *Phyllopora* range from the Ordovician rocks to the Permian. Lastly, in the Carboniferous genus *Goniocladia* the branches anastomose as in *Phyllopora*, but they are keeled on both sides, and there are three or four rows of cells on each side of the median keel on the poriferous side.

The family of the *Acanthocladidæ* comprises a number of Palæozoic *Polyzoa* which are in many respects allied to the *Fenestellidæ*.

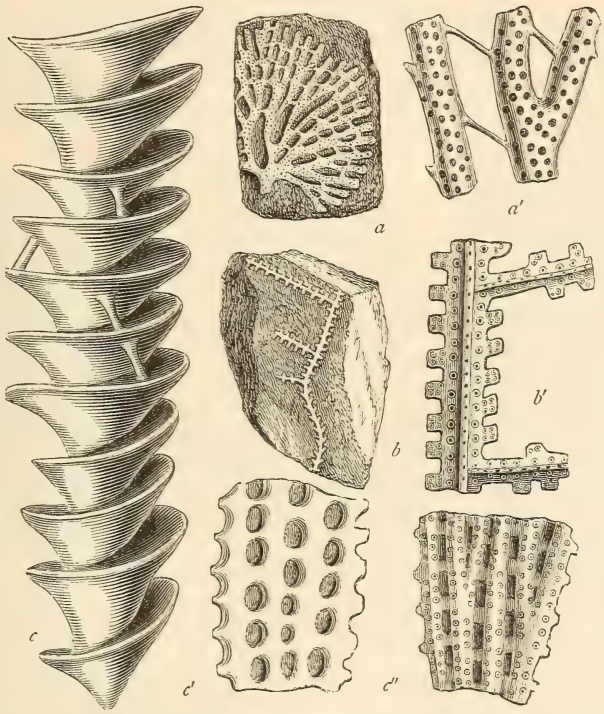


Fig. 471.—Carboniferous *Polyzoa*. *a*, Fragment of *Polypora dendroides*, of the natural size—Ireland; *a'*, Small portion of the same, enlarged to show the cells; *b*, *Pinnatopora* (*Glauconome*) *pulcherrima*, a fragment, of the natural size—Ireland; *b'*, Portion of the same, enlarged; *c*, The central screw-like axis of *Archimedes Wortheni*, of the natural size—Carboniferous, America; *c'*, Portion of the exterior of the frond of the same, enlarged; *c''*, Portion of the interior of the frond of the same, showing the mouths of the cells, enlarged. (After M'Coy and Hall.)

In this family the polyzoary is "poriferous on one side only, dendroid, pinnate, or forming fenestrated expansions, and consisting of strong central stems and numerous smaller lateral branches which proceed from their opposite margins. The lateral branches are free, or may unite (in the fenestrate genera) with those of the adjacent branches. Non-poriferous dissepiments are absent" (Ulrich).

The genus *Acanthocladia* is Carboniferous and Permian, and possesses a polyzoary which is bilaterally branched in a single plane, and which is celluliferous on one side only, the reverse side being solid and striated. The zoœcia are placed on the main stem and branches, and are multiserial. The Carboniferous genus *Pinnatopora* (the *Glauconome* of many authors) resembles the preceding in general form (fig. 471, *b* and *b'*), but the cells are biserial, and the stems have a more or less well-developed keel. The Carboniferous genus *Septopora* resembles *Pinnatopora* generally, but becomes fenestrated by the union of the lateral branches of the polyzoary; while the same thing occurs in the Permian genus *Synocladia*. In this last genus the lateral branches are directed obliquely upwards, and carry two rows of pores each, while the main stems carry from three to five rows of pores separated by a median keel.

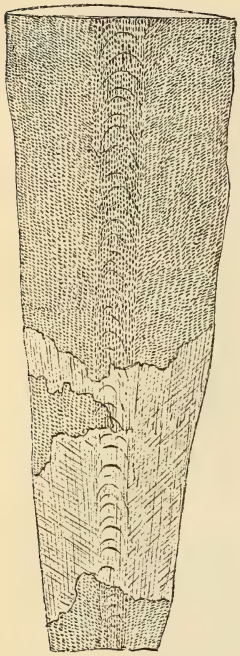


Fig. 472.—A specimen of *Ptilodictya* (*Heterodictya*) *gigantea*, from the Devonian rocks of Canada, of the natural size. The polyzoary is split in half along its median plane, and shows in places portions of the striated calcareous membrane produced by the coalescence of the two layers of cells composing the colony. (Original.)

The families of the *Ptilodictyonidæ*, *Stictoporidæ*, and *Cystodictyonidæ* may be briefly considered together, since they contain Palæozoic *Polyzoa* which are superficially very similar to one another, and which are in many respects really allied, though they differ in the internal structure of the polyzoary. Owing, however, to the fact that various types have been hitherto insufficiently examined by means of microscopic sections, it is not always possible to separate these families accurately, or to refer a particular form to one or other of them. The family of the *Ptilodictyonidæ*, more especially, cannot at present be precisely defined, since the structure of the type-species of the genus *Ptilodictya*—viz., the *P. lanceolata*, Goldf. sp. of the Silurian rocks—has not yet been thoroughly investigated. Judging, however, from external characters alone, it would seem probable that the Devonian Polyzoan described by the writer under the name of *Heterodictya gigantea* is congeneric with *Ptilodictya lanceolata*, as understood by Lonsdale; and we may therefore take the former as exhibiting the essential characters of the genus *Ptilodictya*. The polyzoary in *Ptilodictya* (*Heterodictya*) *gigantea* has the form of a flattened, unbranched, two-edged frond, which reaches several inches in length and an inch or more in width (fig. 472), with a thickness in the centre of about two lines. The polyzoary consists

of two strata of tubular zoœcia, the bases of which unite to form a median calcareous striated layer, along the line of which the frond readily splits. The zoœcia are disposed in parallel longitudinal lines, those of the central rows being themselves longitudinal, while those of the lateral regions of the colony are directed obliquely upwards and outwards, the arrangement of the cells being thus feather-like (fig. 472). The two flattened surfaces of the polyzoary are wholly covered by the minute, oval cell-apertures. As regards the internal structure, the zoœcia have strong, fibrous and imperforate walls, and the cells are traversed by numerous transverse calcareous partitions or "tabulæ," many of which, however, are incomplete, and do not extend the whole way across the tube in

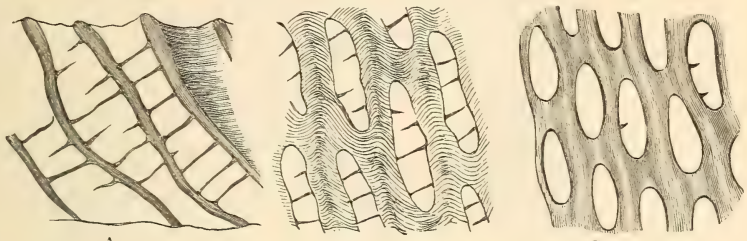


Fig. 473.—Minute structure of *Ptilodictya* (*Heterodictya*) *gigantea*, Nich., from the Corniferous Limestone (Devonian) of Canada. A, Vertical and longitudinal section, showing the well-developed tabulæ; B, Vertical and transverse section, showing the incomplete condition of many of the tabulæ; C, Tangential section. All the figures are enlarged eighteen times. (Original.)

which they occur (fig. 473). The cells run obliquely to the surface, and are in contact throughout, no interstitial tubes or cells being developed.

If the form just described is to be taken as a true *Ptilodictya*, then the essential characters of the genus *Ptilodictya* and of the family *Ptilodictyonidæ* are that the polyzoary is leaf-like, and composed of two layers of tubular zoœcia, which are attached back to back, a spurious mesothecal membrane being formed by the coalescence of their bases; the cells are in contact throughout, no interstitial cells being present; the cell-mouths are simple; and cross-partitions or "tabulæ" are abundantly developed in the tubes. Owing to the uncertainty which at present attaches to the limits of the family *Ptilodictyonidæ*, it is impossible to speak definitely as to the geological range of the family; but *P. lanceolata*, Goldf., is Silurian, and *P.* (*Heterodictya*) *gigantea* is Devonian.

There are various Palæozoic *Polyzoa* that have been commonly placed in the genus *Ptilodictya*, which agree with the preceding in various general characters, but differ in important structural features. Thus,

there are numerous Ordovician and Silurian types, of which we may take *Ptilodictya* (*Stictopora?*) *falciformis* as an example, in which the polyzoary is in the form of an unbranched, or slightly branched, flattened frond (fig. 474, *a*), composed of two layers of cells placed back to back, a more or less recognisable calcareous membrane (the "mesotheca" of Hall) being produced by the coalescence of their bases. In the particular type here selected as an example of this group the polyzoary is usually unbranched, sickle-shaped, and thin-edged, the margins being longitudinally striated, and occasionally perforated by the apertures of minute and imperfect cells. The zoœcia (figs. 474, *c*, and 475, A) are tubular, and in close contact throughout, no interstitial cells being developed;

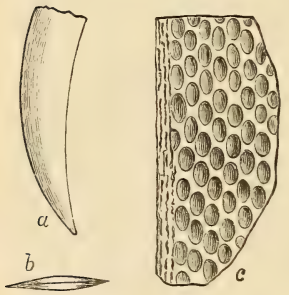


Fig. 474.—*Ptilodictya* (*Stictopora?*) *falciformis*. *a*, Small specimen of the natural size; *b*, Cross-section, showing the shape of the frond; *c*, Portion of the surface, enlarged. Trenton Limestone and Cincinnati Group, America. (Original.)

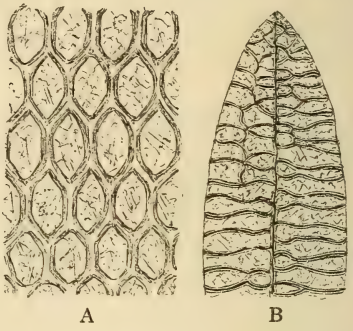


Fig. 475. — Structure of *Ptilodictya* (*Stictopora?*) *falciformis*. A, Tangential section, enlarged, showing the lozenge-shaped tubes; B, Transverse section, enlarged, showing the arrangement of the two layers of cells. (Original.)

and the apertures are oval or lozenge-shaped. The tubes (fig. 475, B) are rectangular to the flat surfaces of the polyzoary, and they do not appear to be traversed by "tabulæ." An essentially similar structure is exhibited by the Silurian Polyzoan described by Hall under the name of *Clathropora frondosa*, which constitutes the type of the genus *Clathropora*. In this case, however, the polyzoary is composite, and is formed by the inosculation of a series of thin leaf-like bilaminar fronds, which anastomose in such a way as to leave regularly placed oval perforations or fenestrules; the minute structure of the tubes resembling that observed in *Ptilodictya falciformis*.

A number of Ordovician, Silurian, and Devonian *Polyzoa*, more or less closely allied in general characters to the types treated of above, have been placed in the family of the *Stictoporidæ*. It does not, however, appear possible at present to give any precise definition of the family, since Hall and Ulrich, who have more especially studied the forms in question, are not agreed as to the limits of the genus *Stictopora*, the type of the whole family. The forms which have been generally included under the name of *Stictopora* are compressed or leaf-like *Polyzoa*, consisting of two layers of cells

placed back to back, and usually more or less branched, the edges of the frond being non-celluliferous, and the cell-mouths being oval or circular.

The family of the *Cystodictyonidæ* is defined by Ulrich as comprising forms of Palæozoic *Polyzoa* in which the polyzoary consists

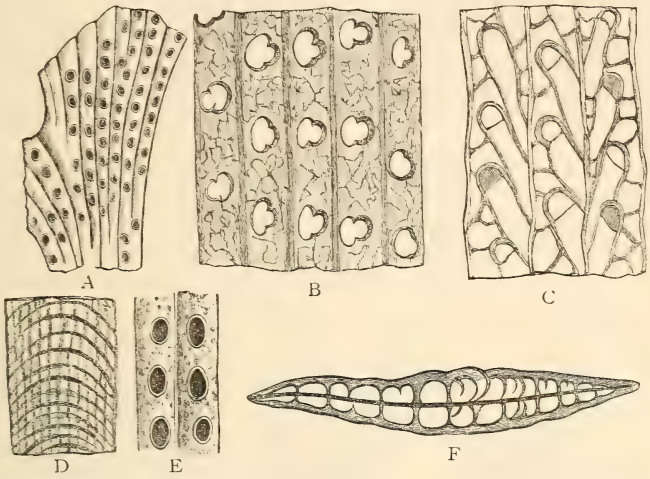


Fig. 476.—*Cystodictya Gilberti*, from the Devonian rocks of North America. A, Part of the polyzoary, enlarged (after Hall); B, Tangential section taken just below the surface, showing the trilobed apertures of the cells; C, Tangential section taken at a deeper level than the preceding, showing the interstitial vesicular tissue; D, Part of a specimen split along the median plane, enlarged; E, Part of the surface, enlarged, showing the porous intercellular tissue; F, Cross-section of the polyzoary, enlarged. (Original.)

of two layers of cells placed back to back, with tubular zoœcia, which are separated by irregular vesicular tissue. The cell-mouths have a small tooth-like projection on each side, giving the aperture a characteristic trilobed form (fig. 476, B); and the margins of the zoarium are sharp or rounded, and are non-poriferous.

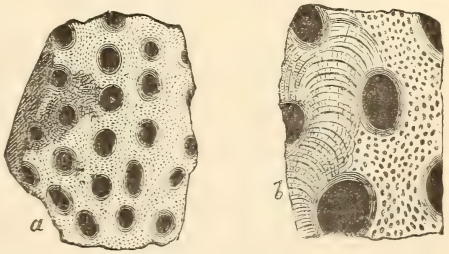


Fig. 477.—Fragment of *Coscinium* (*Coscinotrypa*) *cribriforme*, of the natural size and enlarged. Devonian, Canada. (Original.)

As an example of this family may be taken the Devonian *Cystodictya Gilberti* (fig. 476), in which the polyzoary is irregularly branched, and consists of two layers of cells which open on its opposite surfaces, and are united by a striated mesothecal layer formed by the union of the bases of the

cells (fig. 476, D and F). The cell-mouths are trilobed, and the surface in well-preserved specimens exhibits shallow interapertural pits (fig. 476, E), which in thin sections are seen to be produced by irregular vesicles occupying the intervals between the proper zoœcia (fig. 476, C). This species is abundant in the Devonian rocks of North America, but is placed by Hall in the genus *Stictopora*. The genus *Coscinium* of Keyserling (=*Coscinotrypa*, Hall) possesses an internal structure essentially similar to that of *Cystodictya*, but the polyzoary forms a wide netted expansion (fig. 477), perforated by numerous oval "fenestrules," the edges of which are sharp, and are non-celluliferous. In this genus the interstitial vesicular tissue between the zoœcia is largely obliterated by a finely tubulated calcareous deposit (fig. 455, C).

The family of the *Ceramoporidæ* has been founded by Mr Ulrich for a number of Palæozoic *Polyzoa* in which the polyzoary is usually incrusting, the cell-apertures being triangular or ovate, generally with a prominent and arched lip on one side. The type-genus of this family is *Ceramopora* itself, which ranges from the Ordovician to the Devonian, and forms thin crusts upon corals, shells, &c. The cells

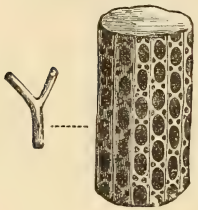


Fig. 478.—Fragment of *Rhombopora Hamiltonensis*, of the natural size and enlarged. Devonian, Canada. (Original.)

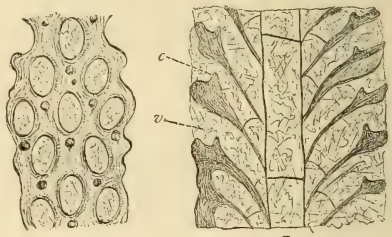


Fig. 479.—*Rhabdomeson gracile*, from the Carboniferous rocks of Scotland. A, Tangential section, enlarged. B, Vertical section, enlarged, showing the central tube: *c*, The proper cell-mouth; *v*, The outer chamber or "vestibule." (Original.)

in this genus are angular, with a strongly arched lip and oblique aperture, and they usually radiate from one or more centres of growth.

Finally, the family of the *Rhabdomesontidæ* includes a number of small Palæozoic *Polyzoa*, in which the polyzoary is ramose, and is composed of slender, cylindrical, solid or tubular branches, the cell-apertures being placed on all sides of the branches (fig. 478). The proper cell-mouth is placed at a little distance below the surface, and opens into a so-called "vestibule" or outer chamber, which constitutes the apparent cell-aperture on the surface (fig. 479, B). The cavities of the zoœcia may be crossed by a limited number of "tabulæ," and the apertures are sometimes provided with perforated "closing-plates"; while thick-walled tubes (for the support

of "avicularia"?) may be developed in the interzoœcial spaces (figs. 479, A, and 455, c).

In the genus *Rhombopora* (fig. 478) the zoœcia radiate in all directions from an imaginary axis, and the proper cell-apertures are placed at the bottom of oval or rhomboidal "vestibules." The species of this genus range from the Silurian to the Carboniferous inclusive. The genus *Rhabdomeson* is principally, if not exclusively, Carboniferous in its range, and comprises forms which are essentially similar to *Rhombopora* in general characters, but differ in the fact that the zoœcia radiate in all directions from an axial calcareous tube (fig. 479, B) running up the centre of the stems.

Sub-Order II. Cheilostomata.

In this sub-order are included all those Gymnolæmatous *Polyzoa* in which the aperture of the cell is subterminal, of less diameter than the cell itself, and usually closed by a movable lip or operculum (fig. 480). The essential character of the *Cheilostomata* is, therefore, the position of the cell-mouth on the anterior face of the zoœcium, instead of at its extremity. The aperture can also be usually closed by a semicircular movable lid, which may or may not be calcified, and which is almost always destroyed in fossilisation. The extent to which calcification of the ectocyst occurs in the *Cheilostomata* varies greatly in different types. Sometimes the polyzoary remains completely corneous (as in the *Flustridæ*), in which case it is incapable of preservation in the fossil condition; whereas in other cases the entire cell-wall may be calcified. There are many forms, however, in which an intermediate state of parts obtains, the hinder and lateral portions of the cell being calcified, while a larger or smaller area of the anterior wall, particularly in the neighbourhood of the mouth, remains in a membranous or horny state. Hence, in such cases the cells, in the fossil condition, are more or less largely open in front. In other cases, where the polyzoary is incrusting, the posterior wall of the cells may be uncalcified.

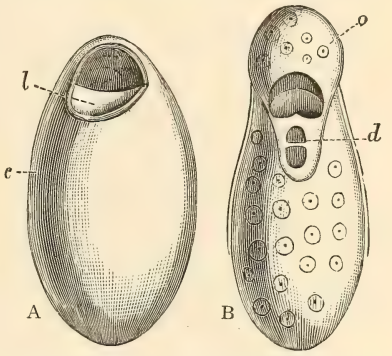


Fig. 480.—Cells of Cheilostomatous *Polyzoa*, enlarged. *c*, Ectocyst; *l*, Operculum; *o*, Ovicell; *d*, immersed avicularium. (After Busk.)

"Avicularia" and "vibracula" are commonly developed in the *Cheilostomata*, and in the case of the living forms afford valuable characters in classification. In fossil forms, however, these minute

appendages can hardly ever be preserved, though their former existence may be inferred from the presence of "special pores" which are usually placed near the mouth, or the existence of thickened tubular supports which penetrate the substance of the polyzoary and are thus recognisable in thin sections (fig. 455, A).

The "ovicells" or marsupial pouches of the *Cheilostomata* are very characteristic structures, though they may be wanting, or may be so deeply immersed in the skeleton as to be inconspicuous. Most usually, the ovicells have the form of globular or helmet-shaped sacs (fig. 480, B) appended to the anterior end of the cells, and placed in communication with the cavity of the latter by special openings.

New cells are produced by budding from the anterior ends or lateral margins of the pre-existing cells, and all the zoœcia remain to some extent directly connected with one another. In the *Cheilostomata* generally contiguous cells are placed in communication with one another by means of perforated portions of their cell-walls ("rosette-plates"), the number and position of these structures varying in different cases. These "rosette-plates" correspond with the pores which are so commonly developed in the cell-wall of the Cyclostomatous *Polyzoa*, but their presence can only be detected in the fossil forms in cases where the condition of preservation is exceptionally good.

As regards the distribution of the *Cheilostomata in time*, it is doubtful, as previously noted, if any representatives of this sub-order have hitherto been detected in the Palæozoic rocks, though there are some Palæozoic types (such as *Paleschara*) which may belong here. On the other hand, in the Secondary rocks, from the Jurassic onwards, we meet with an abundance of the remains of Cheilostomatous *Polyzoa*, while a vast number of Tertiary forms have been described. As the characters which separate the different groups of the *Cheilostomata* are for the most part difficult of recognition, and as the classification of the group is still in a more or less unsettled condition, it will be necessary here to deal with the families of the sub-order very briefly. The arrangement here followed is, in the main, that adopted by Hincks, but only those families which from their size or palæontological significance are of special importance, are alluded to.

In the family of the *Cellulariidæ*, the polyzoary is erect and dichotomously branched, with linear divisions, composed of cells arranged in the same plane. The genus *Cellularia* has no fossil representatives, but *Scrupocellaria* (fig. 457, E) is known both by Recent and Tertiary species.

In the family of the *Cellariidæ* (*Salicornariadæ* of Busk), the polyzoary is erect and dichotomously divided, the branches being cylin-

drical, and the zoœcia disposed round an imaginary axis. The type-genus is *Cellaria* (=*Salicornaria*), in which the surface (fig. 457, c) is divided into rhomboidal or hexagonal spaces, representing the front walls of the cells; and irregularly disposed avicularia are present. The species of this genus range from the Chalk to the present day.

The family of the *Vincularіidæ* is typified by the genus *Vincularia*, the species of which are Cretaceous, Tertiary, and Recent. In this genus (fig. 457, 1) the polyzoary is erect, branched, and rigid, the zoœcia being disposed alternately round an imaginary axis, and having a raised border in front.

The great family of the *Membraniporidæ* includes forms in which there is a calcareous or corneo-calcareous polyzoary, composed of horizontal and contiguous cells, the colony forming an incrusting expansion, or in some cases giving rise to an erect growth. The zoœcia are generally separated by raised margins, the front wall remaining more or less uncalcified. Owing to the membranaceous structure of the anterior walls of the cells, the front of the zoœcia in fossil specimens always appears to be more or less largely open. In the extensive genus *Membranipora* (fig. 481), the cells are surrounded by a well-marked elevated border, the space included within which is technically spoken of as the "area." The entire "area" may be occupied by a horny membrane, in which the true cell-aperture is pierced; and when this is the case, the entire "area" in the fossil condition is open. In other cases a larger or smaller part of the membrane occupying the "area" may be calcified, the remainder being left permanently soft. In these cases the "area" of the cell in fossil examples exhibits a more or less extensive deficiency or "aperture," which is always of greater size than the proper cell-mouth itself. The polyzoary in the genus *Membranipora* is always incrusting, and the numerous species of the genus range from the Chalk to the present day. A similar geological range is possessed by the genus *Biflustra*, in which the polyzoary is generally erect and foliaceous, and is typically composed of two layers of cells placed back to back.

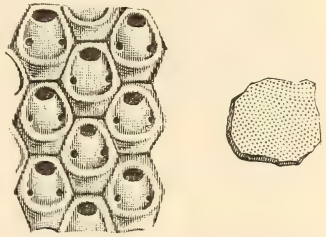


Fig. 481.—*Membranipora oceani*, showing the sub-terminal mouths of the cells. Upper Cretaceous.

In the family of the *Microporidæ* the polyzoary is incrusting, or sometimes free and unilaminar, and the zoœcia resemble those of the preceding family in being surrounded by elevated margins (fig. 482, a), but the front wall of the cells is completely calcareous. The genus *Micropora* (fig. 482, a) comprises forms in which the

cell-mouth is surrounded by a thickened border, and the species contained in it range from the Chalk to the present day.

The family of the *Cribrilinidæ* comprises forms in which the polyzoary is sometimes incrusting, sometimes free and foliaceous. The zoœcia have their front wall more or less fissured, or traversed by radiating ribs separated by intervening furrows, which may be closed or perforated (fig. 482, B). The type-genus of this family is *Cribrilina* itself (=*Lepralia* in part), of which both recent and fossil forms are known, the earliest of the latter appearing in the Cretaceous deposits.

The family of the *Microporellidæ* also includes a number of the incrusting or erect types of *Polyzoa* which were included by older

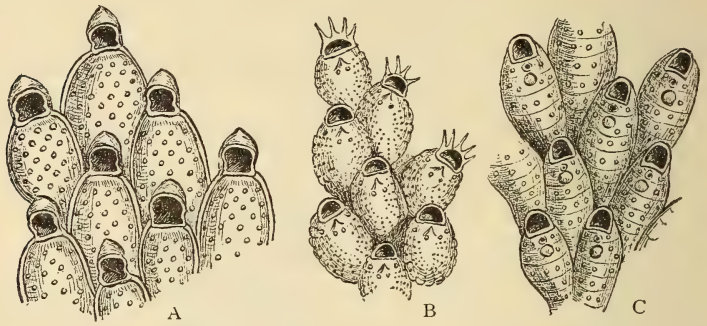


Fig. 482.—A, Cells of *Micropora complanata* (Tertiary and Recent), enlarged; B, Cells of *Cribrilina radiata* (Cretaceous, Tertiary, and Recent), enlarged; C, Cells of *Microporella impressa* (Tertiary and Recent), enlarged. (After Hincks.)

writers under the comprehensive name of *Lepralia;* the essential characters of the family being found in the fact that the cell-aperture is more or less semicircular, with an entire lower margin, while the front wall of the zoœcia exhibits a semilunate or circular "special pore" (fig. 482, C). The type-genus of this family is *Microporella* itself, the species of which are Tertiary and Recent.

The great family of the *Escharidæ* (including under this name also the *Myriozoidæ* of Hincks) comprises forms in which the polyzoary is always completely calcareous, and may be incrusting, or erect and foliaceous, or sometimes dendroid. The zoœcia are without a membranous area or raised margins, the cell-wall being entire or variously punctured, but always without special pores opening into the perivisceral cavity. In the Tertiary and Recent genus *Schizoporella* (fig. 483, B) the polyzoary is sometimes incrusting, sometimes free and foliaceous, and the lower lip of the cell-aperture has a distinct notch or sinus, representing the median pore in the *Microporellidæ*. In the genus *Hippothoa* the form of the cell-mouth is very similar to that seen in *Schizoporella*, but the zoœcia are "dis-

tant, caudate, and connected with one another by a slender prolongation of the lower extremity, so as to form a linear series" (Hincks). The earliest forms of this type appear in the Cretaceous rocks, and the genus still survives. The genus *Eschara*, as formerly understood, has been reconstructed by modern authorities, and its most

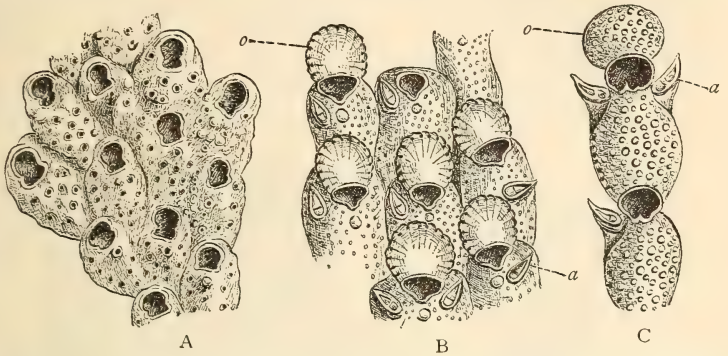


Fig. 483.—A, Cells of *Lepralia pallasiana* (Tertiary and Recent), enlarged. B, Cells of *Schizoporella unicornis* (Tertiary and Recent), enlarged. C, Cells of *Mucronella coccinea* (Tertiary and Recent), enlarged: *a*, Avicularium; *o*, Ovicell. (After Busk and Hincks.)

characteristic forms find a place in the genus *Lepralia*, as at present restricted. In this genus, the polyzoary may be incrusting or erect (fig. 484), and the foliaceous forms may be unilaminar, or may be composed of two layers of cells united back to back. The zoœcia are ovate, with a more or less horse-shoe-shaped aperture, the lower lip of which is entire (fig. 483, A). The species of this genus range from the later Secondary period to the present day. In the genus *Porella*, the original cell-mouth is semicircular, but there is formed round this a secondary and larger mouth which encloses an avicularium. The species of this genus are Tertiary and Recent. The genus *Smittia* (fig. 451, B) resembles the preceding in most characters, but the secondary mouth is elongated and is channelled in front, while the lower lip of the primary aperture is dentate. The species of *Smittia* are Tertiary and Recent. *Mucronella* is another allied genus, in which the peristome (fig. 483, C) is elevated in front into a more or less prominent mucro. The species of the genus are Tertiary and Recent.

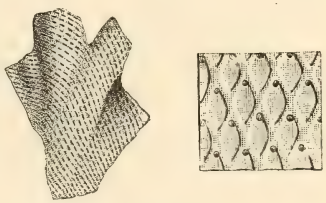
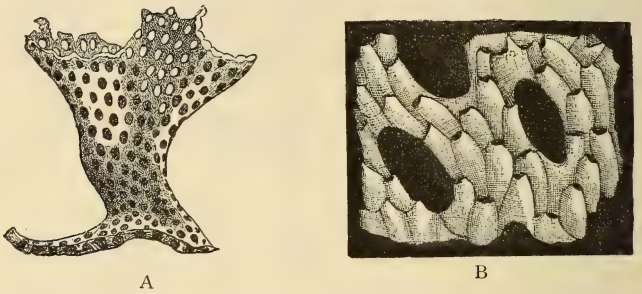


Fig. 484.—*Lepralia* (*Eschara*) *Ranvilliana*. Jurassic.

Related to the preceding, but perhaps forming the type of a separate family (*Reteporidæ*), is the genus *Retepora* (fig. 485), in

which the polyzoary is erect and calcareous, and usually has the form of a reticulate or fenestrated expansion, which is adherent by means of an incrusting base. The zoœcia are developed on the front face only of the zoarium, the dorsal surface being smooth or striated, and carrying avicularia supported upon tubercles. The cells are closely united or immersed, and on the lower margin of the cell-mouth is a prominent rostrum carrying an avicularium. The species of *Retepora* range from the Chalk to the present day.

The family of the *Celleporidæ* includes forms with a calcareous polyzoary, which may be incrusting, or ramose, or massive, and



A B

Fig. 485.—*Retepora cellulosa*, from the Red Crag (Pliocene). A, A fragment, of the natural size; B, Part of the poriferous surface, enlarged. (After Busk—copied from Zittel.)

which consists of irregularly heaped up zoœcia, which are urceolate in form and have sub-terminal mouths. The principal genus in this family is *Cellepora* itself (fig. 457, B), in which the cell-mouths have in their immediate vicinity one or more ascending rostra carrying avicularia. The genus is widely distributed in the Tertiary rocks, and numerous existing species are known.

Lastly, we have the singular family of the *Selenariidæ*, including the allied genera *Selenaria*, *Cupularia*, and *Lunulites* (fig. 457, D), in which the polyzoary is unattached, and consists of a plano-convex or concavo-convex disc, composed of only one layer of cells, the mouths of which open on the convex surface. The three genera above mentioned are the principal ones comprised in this family, and they range from the Chalk to the present day.

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CHAPTER XXXIV.

MOLLUSCOIDEA — continued.

Brachiopoda.

Brachiopoda (*Palliobranchiata*).—The members of this class are defined by the possession of a *body protected by a bivalve shell, which is lined by an expansion of the integument, or "mantle." The mouth is furnished with two long spirally-coiled cirriferous processes or "arms," which act as respiratory organs. The nervous system consists of an œsophageal ring, upon which infra-œsophageal and supra-œsophageal ganglia are developed. One or two pairs of tubular "nephridia" are present, which act as ducts to the reproductive organs. The sexes are distinct or united.*

The *Brachiopoda* are essentially very similar in structure to the *Polyzoa*, from which they are distinguished by the fact that they are never composite, and by the possession of a bivalve, calcareous, or sub-calcareous shell. All the living forms, except *Lingula* (*Glottidia*) *pyramidata* (fig. 486) are fixed in their adult condition to some foreign object, but many of the fossil forms seem to have been permanently free and unattached.

As regards the anatomy of their soft parts, the internal organs in the *Brachiopoda* are enclosed within two integumentary expansions which constitute the "lobes" of the "mantle," and which are generally regarded as being placed on the dorsal and ventral aspects of the body respectively. The space included between these two flaps of the integument is the "pallial cavity," the viscera and muscles being situated towards the beaks of the shell, and separated from the mantle-cavity by a membranous partition, which is perforated by the aperture of the mouth (fig. 487). The larger part of the mantle-cavity is occupied by two long oral processes, commonly spoken of as the "arms," which are the principal organs of respiration, and also serve to bring food-particles to the mouth by the cur-

rents set up by the vibrating cilia with which they are covered. The "arms" are homologous with the tentacular crown ("lophophore") of the *Polyzoa*, and have the form of lateral tubular prolongations of the margins of the mouth, usually of great proportionate length, coiled up spirally and fringed with ciliated lateral processes or "cirri" (fig. 487). In a few forms the arms can be protruded from between the opened valves of the shell, and in many types they are supported upon a more or less complicated

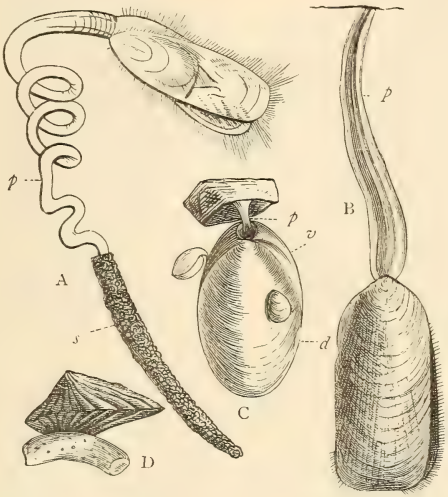

Fig. 486.—Morphology of *Brachiopoda*. A, *Lingula* (*Glottidia*) *pyramidata* (after Morse): *p*, Peduncle; *s*, Sand-tube, encasing base of peduncle. B, *Lingula anatina* (after Cuvier): *p*, The peduncle. C, *Waldheimia cranium*, with adherent young, attached to a stone (after Davidson): *p*, Peduncle; *v*, Ventral valve; *d*, Dorsal valve. D, *Crania Ignabergensis*, attached by its ventral valve to a piece of coral (Chalk).

internal calcareous framework or "loop," the structure of which will be considered in greater detail hereafter.

On the inner side of the cirri of the arms is a ciliated furrow or "brachial groove," which conducts to the opening of the mouth, and which serves for the conveyance of nutritive particles carried in the water-currents set up by the cilia. The mouth conducts by an œsophagus to a globular stomach, surrounded by a well-developed granular "liver." The intestine is sometimes short, sometimes long and coiled, and it may either terminate in a distinct anal aperture (as in *Lingula* and the other genera of Inarticulate Brachiopods), or it may end blindly in the middle line (as in *Terebratula* and the Articulate genera of Brachiopods generally). A distinct heart is present, in some cases at any rate, and has the form of a contractile

vesicle situated on the dorsal side of the stomach. The body-cavity proper is filled with a corpusculated fluid, and sends out branched prolongations into the substance of the pallial lobes. These so-

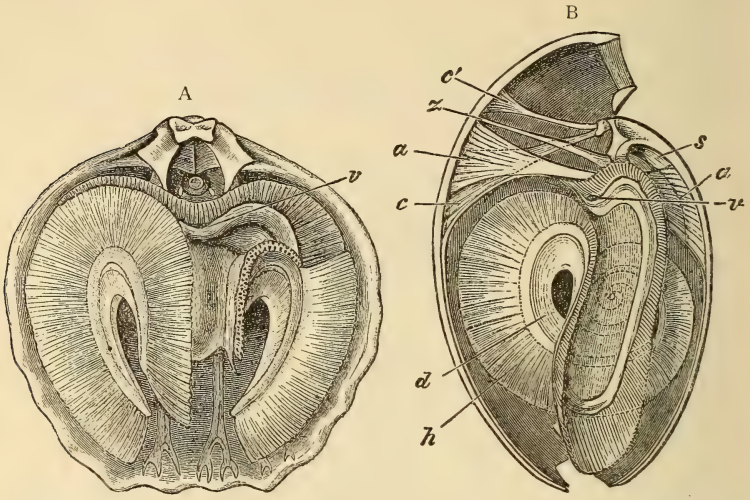

Fig. 487.—Anatomy of *Waldheimia flavescens*. A, View of the animal after the ventral valve of the shell has been removed, enlarged. B, Longitudinal section, enlarged: *d*, Spirally-coiled "arm," with lateral cirri (*h*); *a*, Adductor muscle; *c*, *c'*, Divaricator muscles; *s*, Septum; *v*, Mouth; *z*, Terminal portion of the alimentary canal. (After Davidson.)

called "pallial sinuses" often leave well-marked branching "vascular impressions" on the internal casts of the fossil Brachiopods (fig. 488).

The central nerve-system of the Brachiopods has the form of a

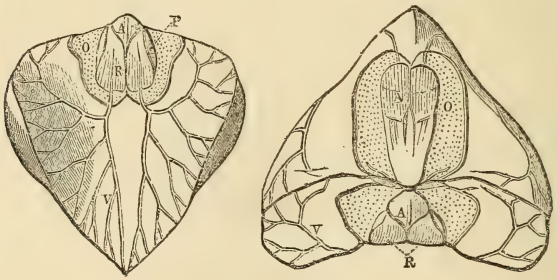

Fig. 488.—Internal cast of *Rhynchonella acuminata*, from the Carboniferous rocks, viewed ventrally and from the umbonal aspect. A, Mark left by the adductor muscle; R, Cardinal muscular impression; P, Mark left by the peduncle; V, "Vascular impressions"; O, Ovarian impressions. (After Davidson.)

circum-œsophageal ring, with a large sub-œsophageal ganglion, and sometimes small supra-œsophageal ganglia as well. The sexes are

sometimes united, but are more commonly distinct, and the reproductive elements reach the exterior by means of two or four tubular "nephridia," which open on the one hand into the body-cavity, and on the other hand into the pallial chamber. The generative glands are developed in the lobes of the mantle, and commonly leave impressions on internal casts of the shell (fig. 488, o). The embryo is ciliated and freely locomotive, but becomes fixed in the course of its development.

The *shell* of the *Brachiopoda* is essentially calcareous, but it may be largely composed of horny matter (as in *Discina*), or the carbonate of lime may be largely replaced by phosphate (as in *Lingula*).

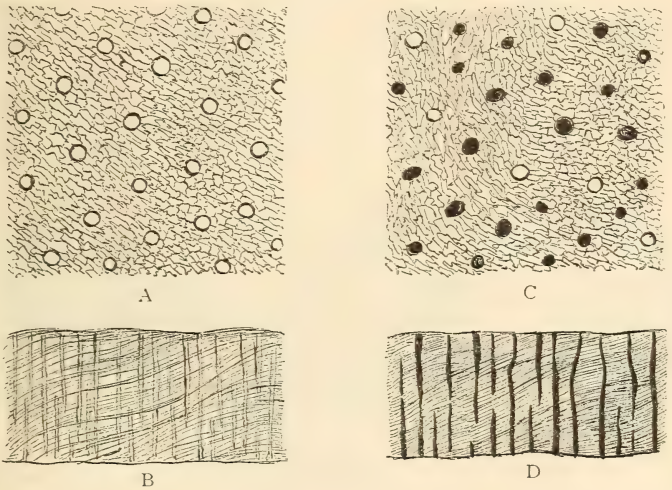

Fig. 489.—Minute structure of the shell of the *Brachiopoda*. A, Tangential section of the shell of the recent *Waldheimia flavescens*, greatly enlarged, showing the tubuli and the ends of the flattened fibrous prisms of the shell; B, Vertical section of the same, less highly magnified; C, Tangential section of the shell of *Cyrtina Hamiltonensis*, from the Devonian rocks of Canada, greatly enlarged, the tubuli being mostly filled with peroxide of iron; D, Vertical section of the same, less highly magnified. (Original.)

In the genus just mentioned, the shell consists of alternating layers of horny and calcareous composition, the calcareous layers being traversed by fine tubuli. As regards its microscopic structure, the shell of the Brachiopods consists of "flattened prisms, of considerable length, arranged parallel to one another with great regularity, and at a very acute angle—usually only about 10° or 12°—with the surfaces of the shell" (Carpenter). The oblique fibrous prisms which compose the shell are best seen in vertical sections (fig. 489, B), but their irregular and closely dove-tailed extremities are also shown in tangential sections (fig. 489, A and C). In some

types of the Brachiopods, as in the genus *Rhynchonella*, the shell-structure is simply fibrous. In many forms, however, the shell is perforated by a series of minute canals, which pass from one surface of the shell to the other, in a more or less vertical direction, being in general more or less dilated just before they reach their termination on the exterior of the shell (fig. 489, B and D). These canals give the shell a "punctated" structure, and in the living animal they contain cæcal tubuli, or solid prolongations, derived from the mantle. In some forms (as in *Producta* and *Chonetes*) the tubuli do not reach the exterior of the shell, the outer layer being simply fibrous. Though the shell is in some groups of the Brachiopods always "punctate," there are nearly allied types in which the shell may be "impunctate" in one case and "punctate" in another. Thus, the shell is simply fibrous in *Rhynchonella*, but is tubulated in the nearly related genus, or sub-genus, *Rhynchoporina*.

The two valves of the shell in any Brachiopod are articulated together by an apparatus of teeth and sockets, or are kept in apposition by muscular action alone. As regards the contained animal,

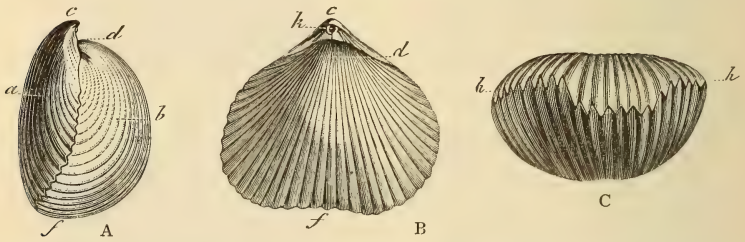

Fig. 490.—*Rhynchonella sulcata.* A, Profile view; B, View of the dorsal surface; C, View of the base. *a*, Ventral valve; *b*, Dorsal valve; *f*, Base; *c*, Beak; *h*, Foramen. Lower Cretaceous.

the position of the valves is anterior and posterior, so that they are properly termed the "ventral" and "dorsal" valves. One of the valves is always slightly, sometimes greatly, larger than the other, so that the shell is said to be "inequivalve" (fig. 490). On the other hand, a line drawn vertically from the beak of the shell to its base (in fig. 490, B, from *c* to *f*) would divide it into two equal halves, so that the shell is said to be "equilateral." In the true Bivalve Shell-fish (*Lamellibranchiata*), on the contrary, the valves of the shell are placed upon the sides of the contained animal, so that they are "right and "left," instead of being dorsal and ventral. Further, the two valves are usually of the same size ("equivalve"), and a line drawn from the beak to the base would almost always divide the shell into unequal halves; so that the shell is "inequilateral."

Ordinarily, the ventral valve of the shell of the Brachiopods is the larger of the two, and it is generally furnished with a prominent curved "beak." Very commonly the beak is perforated by a larger or smaller aperture, which is termed the "foramen" (fig. 490, B), and which serves for the transmission of a muscular peduncle or stem by which the shell is attached to some foreign object. In some cases, however (as in *Lingula*, fig. 486, B), the peduncle simply passes between the apices of the valves, and there is no foramen; whilst in others (as in *Crania*, fig. 486, D), the shell is merely attached by the substance of the ventral valve. The dorsal valve, which is also usually the smaller, is always free, and is never perforated by a foramen. Further, as already remarked, there is reason to believe that some fossil forms were free and unattached in their adult condition.

The *Brachiopoda* are divided into two primary sections according as the valves are held together by muscular action alone, and there is no "hinge" developed ("*Inarticulata*"), or as the valves are pro-

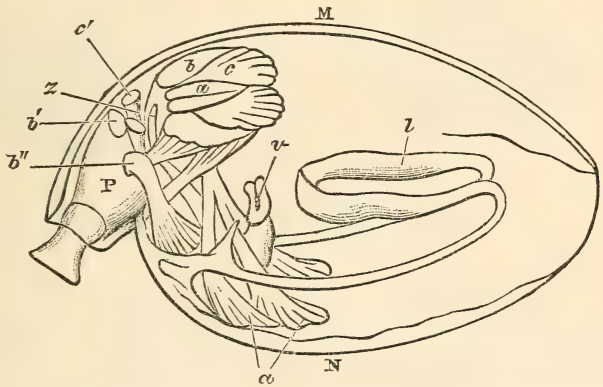

Fig. 491.—Muscular system of *Waldheimia flavescens*. M, Ventral valve; N, Dorsal valve; *l*, Loop; *v*, Mouth; *z*, Extremity of intestine; *a a*, Adductor; *c*, Divaricators; *c'*, Accessory divaricators; *b*, Ventral adjustors; *b'*, Peduncular muscle; *b''*, Dorsal adjustors; P, Peduncle. (After Hancock.)

vided with a proper "hinge" ("*Articulata*"). In the Articulated Brachiopods the valves are united at their beaks by means of two teeth which are developed on the ventral valve, and fit into corresponding sockets in the dorsal valve. Behind the dental sockets of the dorsal valve there is usually a prominent process ("cardinal process"), to which are attached the so-called "cardinal" or "divaricator" muscles (fig. 491, *c*). These are inserted on each side of the centre of the ventral valve, two pairs being usually present; and they serve to open the shell, no structure corresponding with the

"ligament" of the Bivalve Molluscs being developed. One pair of "divaricators" is of much smaller size than the other, and the name of "accessory divaricators" is given to these. The valves, on the other hand, are held together by a pair of "adductor" or "occlusor" muscles (fig. 491, *a*), which pass from one valve to the other, in the neighbourhood of the beaks. The adductors bifurcate about the middle, so as to produce a large quadrangular impression on the internal surface of the dorsal valve (fig. 492, B, *a a*) and a single divided impression towards the centre of the ventral valve (fig. 492, A, *a*). There are also, in some cases, muscles connected with the movements of the peduncle; and others (the "dorsal" and "ventral adjustors"), which have the function of erecting the shell and also that of attaching the peduncle to the shell. In the Inar-

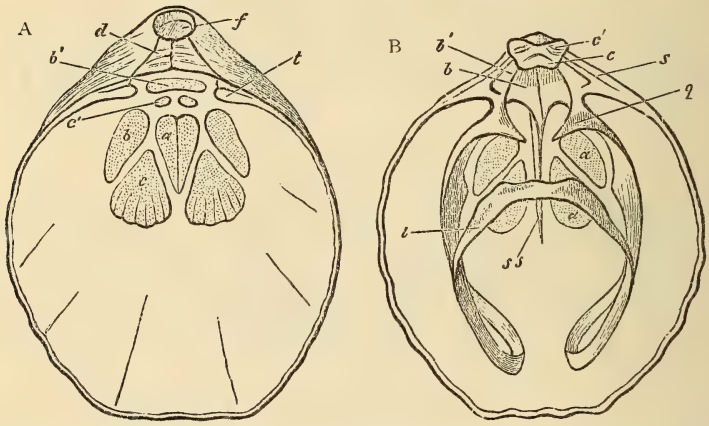

Fig. 492.—A, Interior of the ventral valve of *Waldheimia flavescens*: *f*, Foramen; *d*, Deltidium; *t*, Teeth; *a*, Adductor impressions; *c*, Impressions of the divaricator muscles; *c'*, Accessory divaricators; *b*, "Ventral adjustors"; *b'* Peduncular muscle. B, Interior of the dorsal valve of *Waldheimia flavescens*: *c c'*, Cardinal process; *b b'*, Hinge-plate; *s*, Dental sockets; *l*, Loop; *q*, Crura of the loop; *a a*, Adductor impressions; *c*, Point of attachment of the accessory divaricator; *b*, Point of attachment of the peduncular muscles; *ss*, Septum. (After Davidson.)

ticulated section of the *Brachiopoda*, as in *Lingula*, the arrangement of the muscles by which the valves are opened and shut is still more complicated.

The "arms" or "brachial processes" are in some cases simply coiled up within the shell, but in other cases, as previously noted, they are supported by a more or less complicated calcareous skeleton, which is known as the "loop" or "apophysis" (fig. 492, B). When present, the loop is always attached to the dorsal valve of the shell, and though it serves to support the brachial membrane, it does not strictly follow the course of the arms. In its simplest form, the loop is a thin ribbon-shaped calcareous lamella, the two ends of which

spring from near the hinge of the dorsal valve, while the free end of the loop is folded back upon itself (fig. 492, B). "In some genera it extends to upwards of three-fourths of the length of the shell, as in *Waldheimia*; but in others it is short, and projects but little beyond the hinge-line. In some genera it is attached only to the hinge-plate, as in *Terebratula*, *Waldheimia*, &c.; in others, to a central longitudinal plate or septum, as in *Terebratella*, &c. In certain families the apophysis presents the form of two spirally-coiled lamellæ, which nearly fill the interior of the shell; the ends of the spirals being directed outwards or towards the cardinal angles, as in *Spirifera* (fig. 493), *Athyris*, &c.; or horizontally, the apices facing each other towards the centre of the shell, as in *Glassia*. Again, the spirals are sometimes vertical, their inner sides being pressed together and flattened, with their terminations close together and facing the bottom and centre of the dorsal valve, as in *Atrypa*" (Davidson). The spiral processes are also commonly connected by a more or less complicated system of lamellæ, which vary in shape

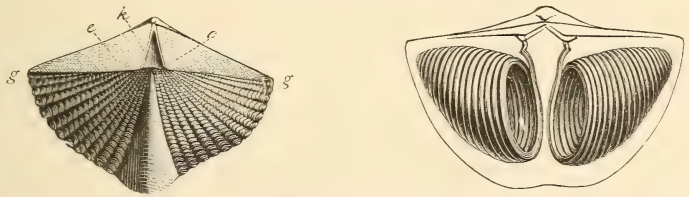

Fig. 493.—*Spirifera hysterica*—Carboniferous. The right-hand figure shows the interior of the dorsal valve, with the calcareous spires for the support of the arms. *g g*, Cardinal angles; *e*, Hinge-area; *k*, Triangular peduncular foramen.

and character in different types, and are of great value in the discrimination of certain genera. In the *Rhynchonellidæ*, the loop is represented only by two short, slender, curved lamellæ; while in some cases the sides of the loop carry minute calcareous spines, showing that even the cirri of the arms were supported by an internal skeleton. In whole families, lastly, as, for example, in the *Strophomenidæ* and *Productidæ*, the arms are entirely devoid of calcified supports.

Very commonly, the beaks of the dorsal and ventral valves of the *Brachiopoda* are separated from one another by a narrower or wider space, which is termed the "hinge-area" (fig. 493, *e*). The "area" is more or less triangular in form, generally developed on the ventral valve only, but sometimes formed by both valves conjointly, and commonly transversely striated. In such genera as *Spirifera* and *Cyrtina* the hinge-area is of very large size, but it may be very narrow, and in many cases it does not exist at all. Another structure that is commonly present in the Articulated Brachiopods

is what is known as the "deltidium." This is a triangular calcareous plate, sometimes single, sometimes composed of two lateral halves (fig. 492, *d*), which is developed in front of the foramen of the ventral valve, and may either completely enclose the foramen (as in *Rhynchonella*), or may simply form the lower boundary of this aperture. What is called a "pseudo-deltidium," again, is a triangular calcareous plate which grows downwards from the upper end of the triangular foramen in such genera as *Spirifera*, and which partially closes this opening.

As regards their *distribution in space*, all the *Brachiopoda* are marine, the number of known existing species and varieties being under one hundred and fifty. The range of the living Brachiopods in depth is very variable, even as regards individual species, some forms commonly living between tide-marks, or in quite shallow water, while others extend to depths of nearly three thousand fathoms. Upon the whole, however, the Brachiopods must be regarded as inhabitants of comparatively shallow water, since about half of the known living species are confined to depths of less than one hundred fathoms.

Leaving the problematical *Eozoön* out of sight, the Brachiopods are amongst the oldest forms of animal life, representatives of this class appearing in the Lower Cambrian deposits. Owing to the great number of fossil Brachiopods, and also owing to the fact that particular types are commonly confined to particular geological horizons, the study of this group of animals is one of great palæontological and stratigraphical importance. Out of one hundred and thirty-nine genera recorded by Davidson, one hundred and six appeared first in the Palæozoic rocks; thirty-four genera are represented in the Mesozoic deposits; and twenty-one in the Kainozoic and Recent deposits taken together. The genera *Lingula*, *Discina*, *Crania*, *Terebratula*, and *Rhynchonella* appear at some point or another in the Palæozoic series, and still exist. About eight genera are represented in the Cambrian; whereas no less than sixty-seven genera are represented in the combined Ordovician and Silurian deposits, after which the number of genera becomes progressively reduced, fifty-two generic types being present in the Devonian, forty in the Carboniferous, and twenty in the Permian. Of the known Mesozoic genera about sixteen are peculiar to this period; while of the thirteen Tertiary genera no less than twelve survive at present; and there are eight exclusively recent genera.

Upon the whole, the hingeless or Inarticulate group of the Brachiopods is the most ancient, all the Cambrian genera, with the exception of *Orthis*, belonging to this division. Of the Cambrian genera, *Lingula*, *Discina*, and *Crania* still survive. While less than one hundred and fifty species exist at present, the united Ordovician and

Silurian systems have yielded nearly two thousand species. Vast as is the number of Ordovician forms, the Silurian rocks are still more rich in this group of fossils; and the class of the *Brachiopoda* may be considered as attaining its maximum in the Silurian period, which has, for this reason, been not unaptly spoken of as the "Age of Brachiopods." In the Devonian rocks more than thirteen hundred species of Brachiopods are known, and though many of these belong to genera which were previously in existence, others belong to types, such as *Uncites*, *Stringocephalus*, *Davidsonia*, &c., which are peculiar to this system of rocks. The great genus *Terebratula* has its first representatives in the Devonian. In the Carboniferous rocks the number of species has undergone a marked reduction, the principal forms belonging to the great Palæozoic families of the *Strophomenidæ*, *Spiriferidæ*, and *Productidæ*. The genus *Producta* attains here its maximum, some of the species having an enormous geographical extension. In the Permian rocks only about thirty species of Brachiopods are known, and these belong mostly to the families of the *Productidæ* and *Strophomenidæ*.

With the beginning of the Mesozoic period, the decay of the Brachiopodous "phylum" which set in during Devonian times becomes still more pronounced. The Triassic rocks, like the Permian, exhibit a singular poverty in the remains of Brachiopods, but the group is fairly represented in both the Jurassic and Cretaceous deposits. Upon the whole, however, the reduction of the number of species which is so marked in the later Palæozoic rocks is progressively continued through the Mesozoic period. Moreover, some of the most characteristic of the Palæozoic families (the *Atrypidæ*, *Trimerellidæ*, *Productidæ*, and *Obolidæ*) have totally disappeared; while the great families of the *Strophomenidæ* and *Spiriferidæ* are only represented by a few surviving types, and disappear wholly in the Jurassic rocks. On the other hand, the families of the *Terebratulidæ* and *Rhynchonellidæ* now assume a marked predominance; the latter, however, being almost exclusively represented by species of the genus *Rhynchonella* itself. Finally, in the Tertiary rocks Brachiopods are few in number, and belong almost wholly to existing *genera*, while a number of the *species* still survive.

As regards *classification*, the *Brachiopoda* may be divided into the two orders of the *Inarticulata* and the *Articulata*, the characters and families of which will be briefly treated of in what follows.

Order I. Inarticulata

(= *Tretenterata*, *Lyopomata*, *Pleuropygia*).

This division of the *Brachiopoda* comprises those forms in which the valves of the shell are not hinged, but are held together by

muscles only, the mantle-lobes are completely free, and the intestine terminates in a distinct anus. This order includes the Palæozoic families of the *Obolidæ* and *Trimerellidæ*, and the three families of the *Lingulidæ*, *Discinidæ*, and *Craniadæ*, which commence in the Lower Palæozoic rocks and are all represented by living species at the present day.

Family 1. Lingulidæ.—In this family the animal is fixed by a muscular peduncle which passes out between the beaks of the valves (fig. 486, B). The shell is almost equivalve, oblong or ovate in form, and composed of alternating corneous and calcareous layers, the latter being phosphatic and perforated by minute tubuli. The arms are fleshy, spirally rolled, and not supported by calcified processes. The family includes the genus *Lingula* along with some allied (sub-generic?) forms, and ranges from the Lower Cambrian to the present day.

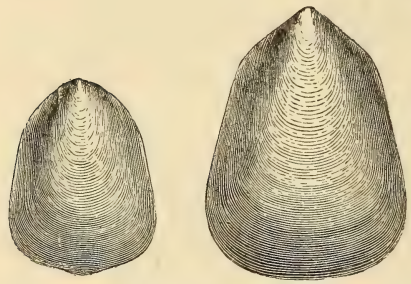

Fig. 494.—*Lingula Eva.* Ordovician. Dorsal and ventral valves. (After Billings.)

In the genus *Lingula* (fig. 494) the shell is oblong, compressed, the dorsal valve little shorter than the ventral. The shell is oval, rounded, or satchel-shaped, tapering more or less towards the beaks. The surface is concentrically striated with lines of growth. The genus commences to be represented in the Cambrian rocks, and has continued without interruption, and with no perceptible change, to the present day.

The genus, or sub-genus, *Lingulella* (fig. 495, D) differs from *Lingula* proper in the fact that there is a distinct groove in the beak of the ventral valve for the passage of the peduncle. This type comprises the oldest of British Brachiopods, *L. ferruginea* being a small form which occurs low down in the Lower Cambrian. Another species—viz., *L. Davisii*—is extremely abundant in the so-called "Lingula Flags" (Upper Cambrian). The sub-genus *Lingulepis* is very similar to *Lingula* proper, but the ventral valve is furnished with a feeble median septum. The type is the *L. pinnæformis* of the Cambrian rocks of North America.

Family 2. Obolidæ.—This family comprises forms closely allied to the preceding, but the beaks of the valves are thickened at their margin, and that of the ventral valve is provided with a groove for the passage of the peduncle. In structure, the shell is calcareo-corneous. The family is principally Cambrian, Ordovician, and Silurian, the genus *Schmidtia* surviving into the Devonian period,

and the genera *Neobolus*, *Lakhmina*, and *Schizopholis* being Carboniferous.

In the genus *Obolus* (fig. 495, B and C) the shell is orbicular, with subequal, smooth valves, the ventral valve having a longitu-

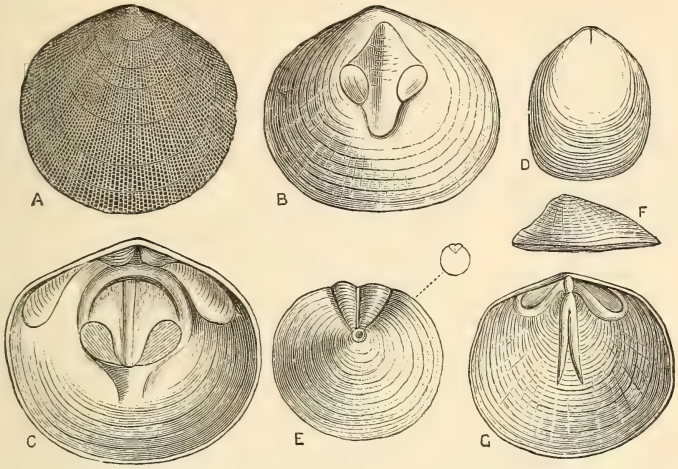

Fig. 495.—*Lingulidæ*, *Discinidæ*, and *Obolidæ*. A, *Trematis filosa*, Ordovician; B, Cast of *Obolus Davidsoni*, Silurian; C, Interior of the dorsal valve of the same; D, *Lingulella Davisii*, Upper Cambrian; E, Ventral valve of *Acrotreta Nicholsoni*, of the natural size and enlarged, and F, Side-view of the ventral valve of the same, enlarged, Ordovician; G, Interior of the dorsal valve of the same. (A is after Billings, and the other figures after Davidson.)

dinal groove for the passage of the peduncle-fibres. Usually there is a weak median septum in the ventral valve. The species of this genus are wholly Ordovician and Silurian, and are especially characteristic of the former of these systems. The little *Obolus Apollinis*

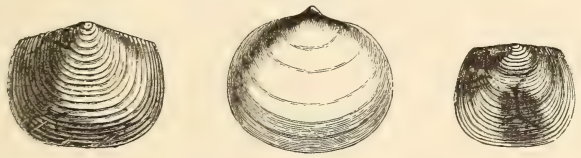

Fig. 496.—*Kutorgina cingulata*. (Billings.) Upper Cambrian.

occurs in vast numbers in the Ordovician "Ungulite Grit" of Russia.

The genus *Obolella*, of the Cambrian and Ordovician formations, is nearly allied to *Obolus*, but the arrangement of the muscular impressions is different. The genus *Kutorgina* (fig. 496) is essentially similar to the preceding, but the shell is sub-quadrate, and there is a straight hinge-line.

The genus is characteristic of the Cambrian rocks of Canada. *Schmidtia*, of the Silurian and Devonian rocks, has a minute oval shell, the ventral valve of which is convex, with a pointed beak below which an "area" is developed; and the genus *Leptobolus* of the Ordovician rocks of North America is closely allied to this, but differs in its internal characters. In the Cambrian genus *Acrothele*, the shell is nearly circular, and the ventral valve is somewhat conical, the beak being sub-central and perforated by a foramen, while the beak of the dorsal valve is marginal.

In the genus *Siphonotreta* (fig. 497) the shell is oval, inequivalve, with unarticulated valves. The beak of the ventral valve is perforated by a foramen which opens on its back, and communicates with the interior by a cylindrical tube. The surface of the shell is covered with concentric lines of growth, and furnished with numerous delicate tubular spines, which, however, are rarely preserved. All the *Siphonotretæ* at present known belong to the Ordovician and Silurian periods.

Fig. 497. — *Siphonotreta verrucosa*. Ordovician.

In the genus *Acrotreta* (fig. 495, E—G) the dorsal valve is nearly flat, and the ventral is conical and patelliform, the surface being concentrically striated. The beak of the ventral valve is perforated by a round foramen, from which a pedicle-groove extends to the posterior margin, and is bounded laterally on either side by a small false area. The genus is wholly Ordovician.

In the neighbourhood of *Acrotreta*, Dr Fischer, with some doubt, places the Silurian genus *Eichwaldia*, which has been commonly referred to the articulate family of the *Rhynchonellidæ*, but in which hinge-teeth and sockets appear to be absent. The shell in this curious genus is subtrigonal or oval, and the ventral valve has its apex perforated by a peduncular foramen, while the dorsal valve is provided with a prominent median septum. The structure of the shell is very peculiar, the most conspicuous feature connected with this being that the greater part of the surface is covered with a special alveolated layer, the hexagonal pits of which are arranged in decussating oblique lines.

Lastly, the Carboniferous rocks of India have yielded certain curious types which have been placed in this family, and have been referred to the genera *Neobolus*, *Lakhmina*, and *Schizopholis*. In all these genera the shell is of small size, and either suborbicular or trapezoidal in shape.

Family 3. Discinidæ.—In this family the shell is corneo-calcareous, with unequal valves, the animal being attached by a muscular peduncle passing through the ventral or lower valve by means of a slit in its hinder portion, or a circular foramen excavated in its substance. The arms (fig. 499) are fleshy and spirally coiled, and are not provided with calcified supports. The *Discinidæ* range from the Ordovician period to the present day.

In the genus *Discina* (figs. 498-500) the shell is sub-orbicular, with conical, nearly equal valves, of which the dorsal is the deepest, while the ventral valve is flatter, and the beaks of both are sub-central. In the typical forms of *Discina*, the ventral valve has an elongated marginal opening, which is prolonged on the surface into an anterior groove traversing the shell obliquely and terminating internally in a second groove which runs in an opposite direction to the first. In the centre of the

ventral valve is a subtriangular plate, which conceals the minute tubular foramen. In the forms which are included in the sub-genus *Orbiculoidea*, the general structure is the same as in *Discina* proper, but the valves are much elevated, and the minute foramen is situated at the posterior extremity of a groove, which is prolonged externally only, but has no internal continuation. The forms comprised in the sub-genus *Discinisca*, again, possess a longitudinal foramen situated between the beak of the

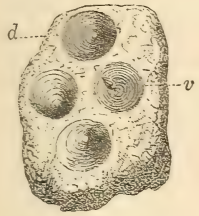

Fig. 498.—*Discina* (*Orbiculoidea*) *nitida*, from the Carboniferous rocks of North America. *d*, Dorsal valve; *v*, Ventral valve. (After Zittel.)

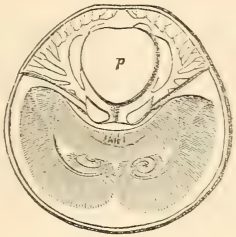

Fig. 499.—The animal of *Discina*, as seen on the removal of the ventral valve and part of the ventral mantle-lobe. *p*, Expanded surface of the peduncle. (After Woodward.)

Fig. 500.—Ventral valve of *Discina Circe*, from the Trenton Limestone (Ordovician) of Canada, showing the pedicle-groove. (After Billings.)

ventral valve and its hinder margin, in the centre of a depressed oval disc, the valve itself being flat or concave. The species of *Discina*, in the general sense, range from the Ordovician to the present day. In the genus *Trematis* (fig. 495, A) both the valves are more or less convex, and the general shape of the shell is sub-orbicular or transversely oval. The dorsal valve is the most convex, its beak being marginal, with a false "area" below it. The ventral valve is flatter, and has a wide mar-

Fig. 501.—*Crania Ignabergensis*. Cretaceous.

ginal slit for the passage of the peduncle. The surface is radiately striated, and is ornamented with small superficial pits. The species of this genus are Ordovician and Silurian.

Family 4. Craniadæ.—In this family the shell is calcareous, more or less circular in shape (fig. 501), the ventral valve being the shallowest, and being usually fixed by the substance of the test

to some foreign object. The dorsal valve is conical or limpet-shaped, and the shell in both valves is tubulated. In the interior of each valve are four principal muscular impressions, formed by the adductors, and in the interior of the ventral valve, centrally, is placed a triangular protuberance, which serves to support the bases of the fleshy arms. The family ranges from the Ordovician to the present day.

The only well-established genus in this family is *Crania* itself, which commenced to exist in the Ordovician period, and which is represented at the present day by several living species. The shell in *Crania* may be smooth, or striated with radiating ribs, sometimes with spines or foliaceous expansions, while the internal margins of the valves are expanded and often granulated. The ventral valve is fixed by its lower surface to foreign bodies, while the free dorsal valve is more or less conical (fig. 501).

In the sub-genus *Pseudocrania* (Ordovician to Devonian), the shell is only slightly inequivalve and is free, while the inner margins of the valves are smooth. In this family may perhaps be placed the singular

Fig. 502. — *Trimerella acuminata* — cast. Silurian. (After Davidson and King.)

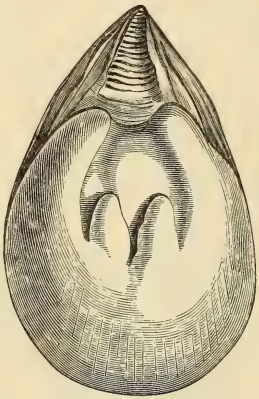

Fig. 503.—*Trimerella grandis*—cast. Silurian. (After Davidson and King.

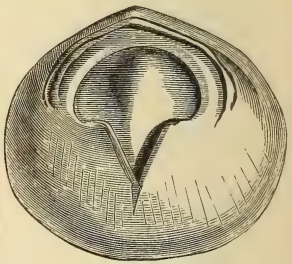

Fig. 504. — *Monomerella prisca*—cast. Silurian. (After Davidson and King.)

Ordovician genus *Schizocrania*, in which the shell resembles *Crania* in general characters, and is fixed by the flattened ventral valve, while the dorsal valve is conical and is radiately striated. The ventral valve, however, exhibits a triangular notch on its posterior side, extending nearly to the centre, and there are six muscular impressions in the dorsal valve.

Family 5. Trimerellidæ.—This family is related to that of the *Obolidæ*, and comprises forms in which the shell is thick and cal-

careous, with unequal valves; the beaks usually prominent, or sometimes obtusely rounded, and either massive and solid, or divided by a partition into two chambers. There is a well-developed hinge-area (fig. 503), and a wide deltidium, bounded by two ridges, the inner ends of which serve as teeth, though true teeth are not present. Each valve is furnished with muscular platforms, which, in the typical species, are elevated and doubly vaulted. The principal, or only, genera of the family are *Trimerella*, *Dinobolus*, and *Monomerella*, and the family is confined entirely to the Ordovician and Silurian rocks. The differences between the above-mentioned genera depend mostly upon internal characters, which can hardly be made clear except by an examination of actual specimens, and as these very generally occur in the form of internal casts, the study of the forms of this group is attended with exceptional difficulties.

Order II. Articulata

(= *Clistenterata*, *Arthropomata*, *Apygia*).

In this order of the Brachiopods the valves of the shell are hinged, usually by means of teeth and sockets; the lobes of the mantle are not completely free; and the intestine ends blindly. This order includes the families of the *Productidæ*, *Strophomenidæ*, *Koninckinidæ*, *Spiriferidæ*, *Atrypidæ*, *Rhynchonellidæ*, *Terebratulidæ*, *Stringocephalidæ*, and *Thecidiidæ*, of which only the *Rhynchonellidæ*, *Terebratulidæ*, and *Thecidiidæ* are represented by living forms.

Family 1. Productidæ.—In this family the shell is entirely free, or is attached to submarine objects by the substance of the ventral valve or by means of spines. The valves may be regularly articulated, or may be kept in place by muscular action alone. There is a straight hinge-line, and the outer surface is more or less largely furnished with tubular spines, while the inner surface exhibits numerous funnel-shaped punctures. The arms are not provided with calcified supports, but there are well-marked muscular and vascular impressions. The ventral valve (fig. 505, *ve*) is convex, while the dorsal valve (*do*) is concave, and is furnished with a prominent cardinal process (*ca*), to which the divaricator muscles are attached. The interior of the dorsal valve exhibits a pair of large central dendritic adductor-impressions, separated by a median ridge (*a a*), a pair of reniform vascular impressions (*i*), and two shelly prominences (*p*), which probably served to support the bases of the arms. The interior of the ventral valve exhibits a pair of large dendritic adductor-impressions, situated close beneath the incurved beak, a pair of large lateral striated divaricator-impressions (*d d*), and two anterior depressions (*s*) which probably lodged the spiral arms.

All the members of the *Productidæ* are Palæozoic, the earliest forms appearing in the Silurian, while the last are found in the Permian deposits.

In the genus *Producta* (or *Productus*) itself (figs. 505-507) the valves are not articulated by teeth and sockets, and appear to have been generally free in the adult condition. In some cases, however, where the shell is furnished with long spines, it may be supposed that these structures served to moor the animal in the soft ooze of the sea-bottom. In the curious *Producta complectens*, Mr R. Etheridge, jun., has shown that the shell was firmly attached by the

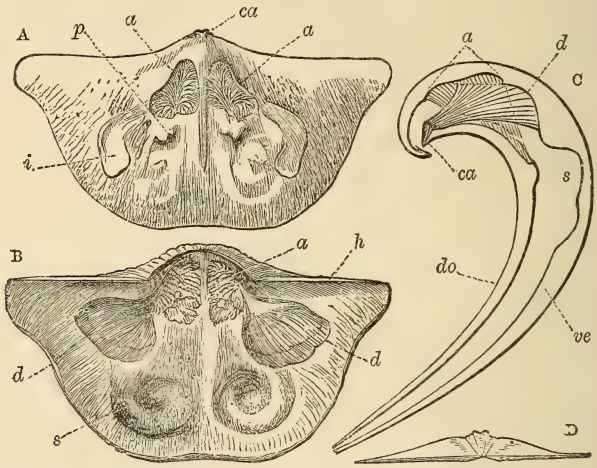

Fig. 505.—Structure of *Producta gigantea*, from the Carboniferous Limestone. A, Interior of the dorsal valve; B, Interior of the ventral valve, a portion of the projecting beak being removed; C, Ideal section of both valves, in place, in the middle line; D, Hinge-line of the dorsal valve. *a a*, Adductor impressions; *d d*, Divaricator impressions (in the ideal fig. C the letters *a* and *d* indicate the adductor and divaricator muscles respectively); *i*, Reniform vascular impressions; *p*, Processes supporting the bases of the arms; *s*, Hollows occupied by the spiral arms; *ca*, Cardinal process; *h*, Hinge-line; *do*, Dorsal valve; *ve*, Ventral valve. (After Woodward.)

twisting of some of the spines of the ventral valve round the column of a Crinoid. In the still more singular *Producta proboscidea*, the ventral valve is prolonged beyond the dorsal, and its edges are rolled together and form an elongated tube, by which the shell was attached to some foreign body. The shell in *Producta* is generally transversely elongated in shape, and is "auriculate" or furnished with ear-like expansions. There is a straight hinge-line, usually shorter than the greatest width of the shell, the hinge-area being linear or wanting. The ventral valve is convex, with a large, bent, and imperforate beak—the dorsal valve being concave, and following the curve of the former. The surface is ribbed or striated, and

the ribs carry a larger or smaller number of longer or shorter tubular spines, which are especially abundant upon the auricular expansions. The species of *Producta* range from the Devonian to the Permian, but the genus is essentially and especially characteristic of the Carboniferous period.

The genus *Strophalosia* (fig. 508, B) ranges from the Devonian to the Permian, and is distinguished from *Producta* chiefly by the fact that the

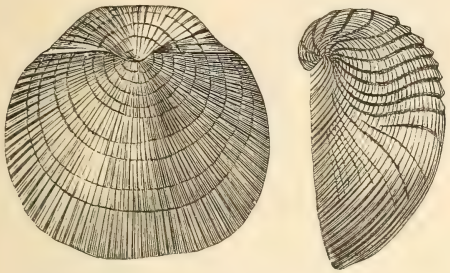

Fig. 506.—Dorsal and profile views of *Producta semireticulata*. Carboniferous.

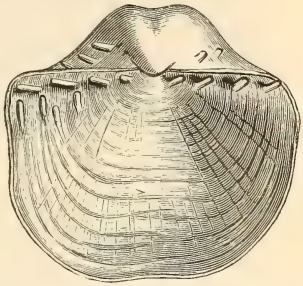

Fig. 507.—Dorsal aspect of *Producta horrida*. Permian. (After King.)

valves are not edentulous, but are articulated by teeth and sockets; while each valve has a distinct hinge-area, and the ventral valve has a foramen covered with a deltidium. *Aulosteges*, again (fig. 508, A), from the Permian, has no teeth or dental sockets—in this respect agreeing with *Producta*—but the ventral valve has a wide hinge-area, pierced by a foramen, which is covered by a convex pseudo-deltidium. *Aulosteges* is probably only a sub-genus of *Strophalosia*, but the shell is free, whereas

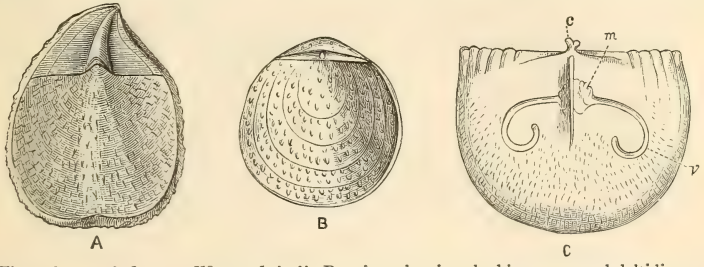

Fig. 508.—A, *Aulosteges Wangenheimii*—Permian, showing the hinge-area and deltidium; B, *Strophalosia Goldfussi*, viewed dorsally—Permian; C, *Productella onusta*—Devonian—interior of the dorsal valve, showing the cardinal process (*c*), the muscular scars (*m*), and the reniform vascular impressions (*v*). (After Davidson and Hall.)

in the latter the shell is attached by the beak of the ventral valve. Lastly, in the Devonian *Productella* (fig. 508, C) the valves are articulated by teeth and sockets, and a hinge-area is present in both valves, but the latter is narrow and linear, and the ventral valve is extremely convex and gibbous.

In the genus *Chonetes* (fig. 509) the shell is concavo-convex, trans-

versely oblong, with a straight hinge-line. The hinge-line is as wide as the shell, or the shell is eared. The ventral valve is convex, the dorsal concave, and both have a distinct hinge-area, with a central fissure, closed in the ventral valve by a pseudo-deltidium. The upper edge of the hinge-area of the ventral valve is furnished with a row of delicate

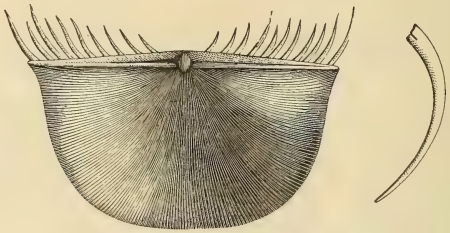

Fig. 509.—*Chonetes Dalmaniana.* Carboniferous.

tubular spines. The species of *Chonetes* are distributed in the Silurian, Devonian, and Carboniferous periods.

Family 2. Strophomenidæ.—In this great family of Brachiopods the shell is rounded or subquadrate, generally compressed, plano-convex, concavo-convex, or biconvex, the beaks being rarely prominent, and the hinge-line being straight and long. The shell seems usually to have been attached by a muscular peduncle. There is a low hinge-area in each valve, often with a triangular fissure, sometimes closed by a pseudo-deltidium, beneath the beaks. The

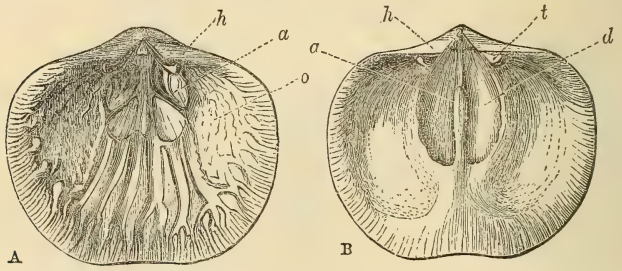

Fig. 510.—Interior of the dorsal valve (A) and ventral valve (B) of *Orthis striatula*, from the Middle Devonian of the Eifel. *h*, Hinge-area; *t*, Hinge-teeth; *a a*, Adductor impressions; *d*, Impressions of the divaricators and peduncle-muscles; *o*, Ovarian spaces. (After Davidson.)

ventral valve has two powerful hinge-teeth (fig. 510, *t*); and the dorsal valve has a prominent cardinal process, between two short brachial processes. The interior of the dorsal valve (fig. 510, A) exhibits four adductor-impressions (*a*), and well-marked vascular impressions which enclose wide ovarian spaces (*o*). The interior of the ventral valve (fig. 510, B) shows two narrow, centrally-placed

adductor-impressions (*a*), flanked by fan-shaped scars (*d*) produced by the conjoined divaricators and peduncle-muscles, the whole enclosed in a saucer-shaped depression. The arms are devoid of spiral supports, and the shell is usually penetrated by microscopic tubuli, which are comparatively large and remote.

The three principal genera of the *Strophomenidæ* are *Strophomena*,

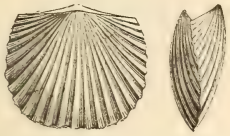

Fig. 511.—*Orthis calligramma*, var. *Davidsoni*; dorsal and side view. Ordovician.

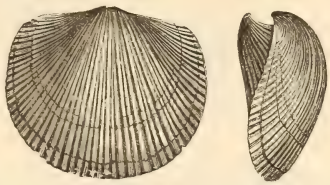

Fig. 512.—*Orthis porcata*; dorsal and side view. Ordovician.

Orthis, and *Leptæna*, and with the doubtful exception of some Mesozoic forms of the last of these, the entire family is confined to the Palæozoic period.

In the genus *Orthis* the valves are articulated by teeth and sockets, and usually are more or less transversely oblong (figs.

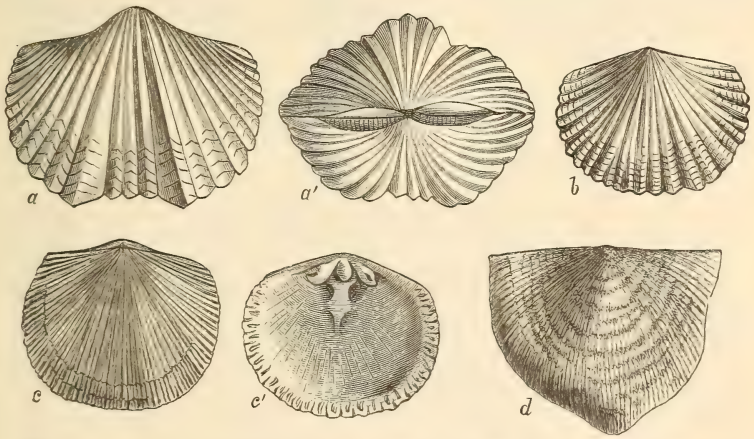

Fig. 513.—*a* and *a'*, *Orthis* (*Platystrophia*) *biforata*, Ordovician; *b*, *Orthis flabellulum*, Ordovician; *c* and *c'*, Exterior and interior of the dorsal valve of *Orthis subquadrata*, Ordovician; *d*, *Strophomena deltoidea*, Ordovician. (After Meek, Hall, and Salter.)

510-514). There is a straight hinge-line, generally shorter than the width of the shell. Each valve has a hinge-area, notched in its centre by a triangular fissure through which the fibres of the peduncle were transmitted. The shell is often more or less flattened or depressed, and the surface may be smooth, but is more commonly

ornamented with striæ, or furnished with well-marked longitudinal ribs. The species of the genus *Orthis* begin in the Cambrian, and abound in the Ordovician, Silurian, Devonian, and Carboniferous periods, especially in the first two of these; but the genus is not known to have survived the Carboniferous period. This genus is one of the most important and widely distributed groups of Palæozoic Brachiopods, and the species belonging to it may generally be distinguished from the closely related *Strophomenæ* by the fact that the shell is seldom flat, one valve being usually much more convex than the other; while the general form is compact and not extended, and the hinge-line is often shorter than the greatest width

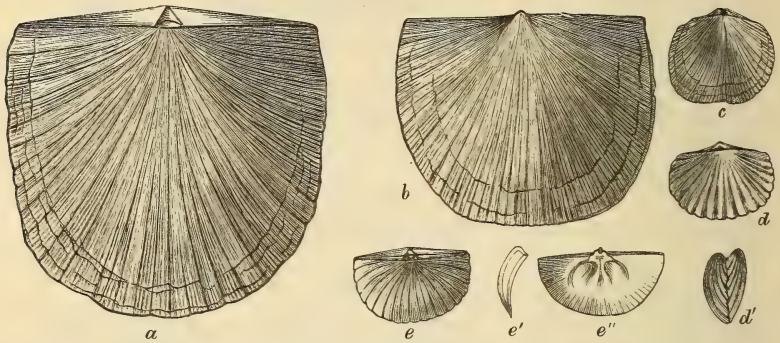

Fig. 514.—*a*, Dorsal aspect of *Strophomena alternata*, from the Ordovician of North America; *b*, Ventral aspect of *Strophomena filitexta*, Ordovician, North America; *c*, *Orthis testudinaria*, Ordovician; *d d'*, *Orthis plicatella*, Ordovician; *e e' e''*, *Leptæna sericea*, Ordovician. (After Meek, Hall, and the Author.)

of the shell. The muscular scars are quadrate, and not extended either vertically or laterally. Lastly, the "cardinal process"—that is, the projection of the dorsal valve, to which the "divaricator muscles" are attached—is undivided and linear. Though the species of *Orthis* most nearly resemble certain forms of *Strophomena*, and are very liable to be confounded with these, one or two species (such as *Orthis biforata*—513, *a*) closely simulate the genus *Spirifera* in general form.

In the sub-genus *Platystrophia*, of which *Orthis biforata* of the Ordovician rocks (fig. 513, *a*) is a characteristic form, the shell is generally transversely elongated, with a long hinge-line, both valves convex, and the ventral valve with a deep median sinus. A hinge-area and triangular deltidial fissure are present in both valves. The valves are radially plaited, and the beaks are prominent and incurved. The sub-genus ranges from the Ordovician to the Carboniferous.

The genus *Skenidium* (fig. 515, D—G) is in many respects allied to *Orthis*, but the ventral valve is much elevated, with a high triangular

area, in the centre of which is a deltoid foramen often partially closed by a pseudo-deltidium ; while the dorsal valve is furnished with a prominent median septum, which is continuous with the cardinal process superiorly, and may be bifurcated at its anterior extremity. The species of *Skenidium* are Ordovician and Silurian, and it seems probable that the genus is identical with the Devonian *Mystrophora* of Kayser.

In the Silurian and Devonian genus *Tropidoleptus* (fig. 515, A—C), the

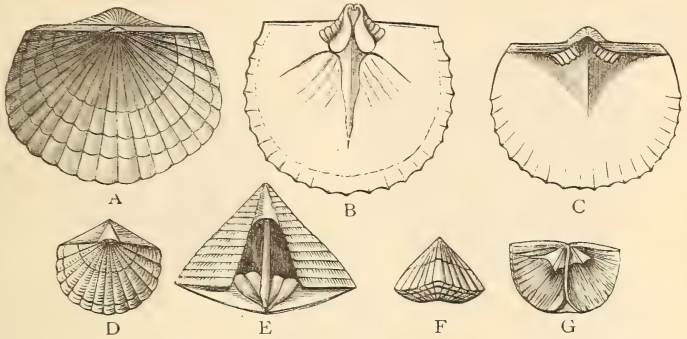

Fig. 515.—A, Dorsal view of the shell of *Tropidoleptus carinatus*, Devonian (Hamilton group) of North America, of the natural size ; B, Interior of the dorsal valve of the same ; C, Interior of the ventral valve of the same ; D, Dorsal aspect of *Skenidium insigne*, from the Silurian (Lower Helderberg) of North America ; E, Cardinal aspect of the same enlarged, showing the high area of the ventral valve, and the triangular foramen partially closed by a pseudo-deltidium ; F, Base of the same ; G, Interior of the dorsal valve of the same, showing the median septum. (After Hall.)

shell is concavo-convex, radiately ribbed, with a straight hinge-line and a double area, that of the ventral valve perforated by a large foramen. The ventral valve carries two strong, crenulated and diverging teeth, and the dorsal valve has two correspondingly crenulated dental sockets, a well-marked median septum, and a prominent cardinal process which almost entirely fills the foramen in the ventral valve. The species of *Tropidoleptus* are Silurian and Devonian.

In the genus *Orthisina* (= *Klitambonites* and *Hemipronites*) the shell resembles that of *Orthis*, but the ventral valve is pyramidal, and has a very high area, directed more or less at right angles to the median plane of the valves, while the dorsal valve is furnished with a smaller area. In both valves there is a triangular fissure in the hinge-area, covered by a pseudo-deltidium, that of the ventral valve being often perforated by a peduncular foramen. The typical forms of *Orthisina* are found in the Ordovician deposits.

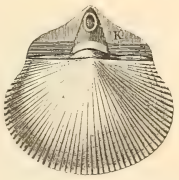

Fig. 516. — *Orthisina Verneuili.* Ordovician.

In the genus *Strophomena* (figs. 513, 514, and 517) the shell is depressed, generally semicircular, the hinge-line as long as the width of the shell, or longer. The surface may be smooth, but is most commonly striated or ribbed. There is a double hinge-area, which is largest in the ventral valve. Each hinge-area has a median notch,

which, in the ventral valve, is partially covered by a deltidium. The ventral valve may be convex or concave, and the dorsal valve follows the curvature of the ventral valve. The species of the genus *Strophomena* are very abundant in the Ordovician, Silurian, Devonian, and Carboniferous formations, often attaining a large size; but they do not seem to have survived the close of the last-named period.

Speaking generally, the species of *Strophomena* may be distinguished from those of *Orthis* and *Leptæna*—both of which they

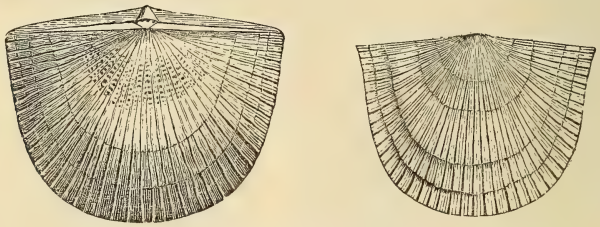

Fig. 517.—*Strophomena antiquata.* Ordovician and Silurian.

much resemble occasionally—by attention to the following points: The shell is *usually* flat and semi-oval, its length and breadth being about equal, and the hinge-line always equalling and often exceeding in length the transverse diameter of the shell. Rarely, the shell is bent and transversely extended, as in *Leptæna*. The cardinal process is large and bifid; and the muscular impressions are quadrate and laterally expanded.

The name of *Strophodonta* has been given to forms of *Strophomena* in which the hinge-line is crenulated, and there is no fissure in the hinge-

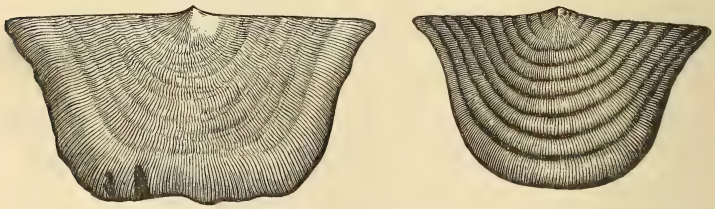

Fig. 518.—*Plectambonites* (*Strophomena*) *rhomboidalis.* Silurian.

area of the ventral valve. The name of *Plectambonites* (*Leptagonia*), again, has been given to forms of *Strophomena* in which the shell is concavo-convex, transversely semicircular, radially striated, and often concentrically wrinkled in the neighbourhood of the beaks (fig. 518). The valves in these types are generally strongly geniculated, the umbonal region being flattened, while the margins of the shell are bent towards the dorsal aspect. Forms belonging to this group are found in the Ordovician, Silurian, Devonian, and Carboniferous formations; a typical

example, and one of very wide geographical range, being the familiar *Plectambonites* (*Strophomena*) *rhomboidalis* (fig. 518), which begins in the Bala beds (Ordovician), and survived into the Carboniferous period.

The genus *Streptorhynchus* (*Orthotetes*) comprises forms like *Strophomena*, with a biconvex or concavo-convex, radially striated shell. The beak of the ventral valve is long, often twisted, with a high area and a pseudo-deltidium ; the area of the dorsal valve being linear. The genus ranges from the Devonian to the Permian, characteristic species being the *S. umbraculum* of the Middle Devonian and the *S. crenistria* of the Carboniferous.

In the genus *Leptæna* are forms smaller than the majority of the *Strophomenæ*, but in many respects resembling these. The shell is more or less completely semicircular (figs. 514, *e*, and 519), transversely elongated, with a double hinge-area, notched in the centre, the fissure in the ventral valve having a deltidium, and the surface being generally striated. Speaking generally, the species of *Leptæna* can usually be separated from those of *Strophomena* or *Orthis* by the form of the transversely elongated shell, the valves of which are strongly bent, so that one (the dorsal) is always very concave, and the other (the ventral) correspondingly convex. Moreover, the muscular impressions are elongated instead of being laterally expanded, as they are in the genus *Strophomena*. The genus *Leptæna* ranges from the Ordovician to the Carboniferous. A few forms from the Lower Jurassic rocks have also been referred to the genus *Leptæna*, but some of these are now placed in the succeeding family, in the genus *Koninckella*, and it is very doubtful if the others are properly referable to *Leptæna*.

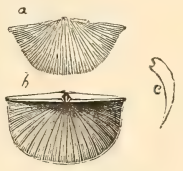

Fig. 519.—*Leptæna sericea*. *a*, Ventral valve ; *b*, Dorsal valve ; *c*, Section of the shell. Ordovician.

Finally, the genus *Davidsonia* includes certain singular Brachiopods, in which the shell is thick and solid, and is attached to foreign bodies by the substance of the ventral valve. The ventral valve has a wide area, with a triangular fissure covered by a convex deltidium; and though there are no calcified brachial supports, the position of the arms is indicated by two spirally-grooved elevations in the interior of the valve. The species of *Davidsonia* are found in the Devonian rocks, and the genus should perhaps be referred to the following family.

Family 3. Koninckinidæ.—This family is incompletely known, and includes small Brachiopods, in which the shell is plano-convex or concavo-convex, the hinge-line being straight or curved, and a hinge-area being absent. There may or may not be a foramen in the beak of the ventral valve, and the arms are supported upon two loosely-inrolled spiral lamellæ, the apices of the coils being directed towards the ventral valve. The typical forms of this family range

from the Devonian to the Lias, but the Silurian genus *Cœlospira* may possibly belong here.

In the genus *Koninckina*, comprising only the *K. Leonhardi* (fig. 520) of the Upper Trias, the shell is circular, concavo-convex in form, very thick, with a smooth surface and an impunctate shell-structure. The hinge-line is straight, with teeth and sockets, but without an area or deltidium. The ventral valve is very convex, and a large part of the cavity of the shell is occupied by the spirally-coiled brachial processes. Nearly allied to *Koninckina* is the Devonian genus *Anoplotheca*, in which the spirals for the arms are more largely developed than in the former.

Lastly, the genus *Koninckella* has been founded by Munier-Chalmas for the reception of some of the small Brachiopods of the Lias which

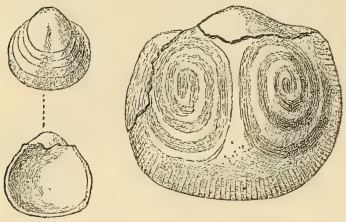

Fig. 520.—*Koninckina Leonhardi*, from the Trias of St Cassian. The left-hand figures show the ventral and dorsal aspects of the shell, of the natural size. The right-hand figure is enlarged, and shows the spiral brachial processes. (After Zittel.)

Fig. 521.—*Koninckella liasina*. Lias. The small cross below the figure indicates the real size of the shell.

were formerly referred to *Leptæna*. In this genus the shell (fig. 521) is concavo-convex, smooth, and in general aspect not unlike a *Leptæna*, but the arms are supported by spiral brachial processes of two or three coils, which carry lateral calcareous spines for the support of the cirri of the arms. The type of this genus is the *Koninckella liasina* of the Lias.

Family 4. Spiriferidæ.—In this family the shell is biconvex, its minute structure being sometimes punctated, sometimes fibrous. The arms were entirely supported upon two spirally-rolled calcareous lamellæ, which spring from the hinge of the dorsal valve—the bases of the spires being turned towards each other, while their apices are directed laterally towards the cardinal angles of the shell (fig. 493).

The family of the *Spiriferidæ* is pre-eminently Palæozoic, but several forms extend into the older Secondary rocks. No member of the family, however, has yet been found in rocks younger than the Lias. Of the genera of the family, the most important is the genus *Spirifera*, or *Spirifer* (figs. 522, 523, 524, and 526), in which the valves are articulated by teeth and sockets, and the shell is not punctated. The hinge-line is long and straight, and the well-marked hinge-area is divided across in each valve by a triangular fissure,

which in the ventral valve is closed more or less completely by a pseudo-deltidium, and in the dorsal valve is occupied by the cardinal process. The true Spirifers are mainly Silurian, Devonian, and Carboniferous, and the forms of the second of these formations often have the shell winged, or drawn out at the lateral angles (fig. 523). In the Permian rocks a few species of the genus are found. The forms included under the name of *Spiriferina* (fig. 525) range from the Devonian to the Lias, and differ from *Spirifera* proper in

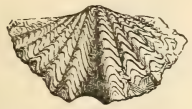

Fig. 522.—*Spirifera sculptilis.* Devonian.

Fig. 523.—*Spirifera mucronata.* Devonian.

the fact that the shell is punctated, and in the presence of a strong median septum in the ventral valve between the dental plates, while the surface of the shell is usually covered with small tubular spines.

Suessia, of the Lias, resembles *Spirifera* in general form, and in the impunctate structure of the shell, and agrees with *Spiriferina* in the possession of a median septum between the dental plates in the ventral valve, while the "crura" of the brachial spirals are united by a transverse band. The Carboniferous *Syringothyris*, again, resembles *Spiriferina* in the punctation of the shell; but the upper ends of the dental lamellæ

Fig. 524.—*Spirifera Niagarensis.* Silurian, America.

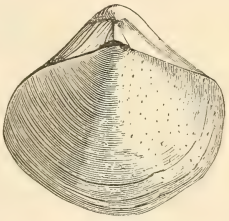

Fig. 525.—*Spiriferina rostrata.* Lias.

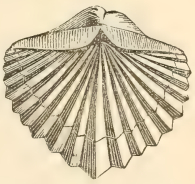

Fig. 526.—*Spirifera trigonalis.* Carboniferous Limestone.

are connected with two horizontal plates, which bend downwards in the middle line, and form by their apposition a tubular fissure beneath the beak of the ventral valve.

In the genus *Cyrtia* the shell resembles *Spirifera* in most respects; but the valves are very unequal, the dorsal valve is approximately flat, and the ventral valve is pyramidal, with a very large triangular hinge-area and a long and narrow foramen, which is partially closed by a pseudo-deltidium. *Cyrtina* (fig. 527, C and D) resembles *Cyrtia* in the shape of the valves, but the shell is punctate, whereas in the latter it is

impunctate. The genus *Cyrtia* is Silurian and Devonian, a familiar species being the *C. exporrecta* of the Wenlock Limestone, while the species of *Cyrtina* range from the Devonian to the Trias.

More important than either of the preceding is the genus *Athyris* (including under this head the *Spirigera* of D'Orbigny), which

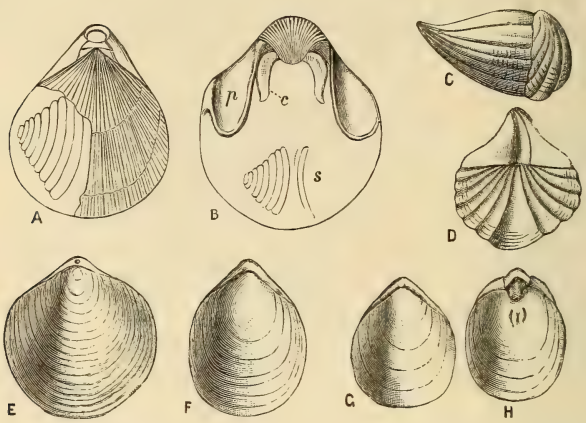

Fig. 527.—A, *Retzia serpentina*, with part of the dorsal valve removed to show the spires; *b*, *Uncites gryphus*, with the spires (*s*), from the Devonian; C, Side view of *Cyrtina heteroclita*—Devonian; D, The same viewed from the dorsal aspect; E, *Athyris concentrica*—Devonian; F, *Merista lævis*—Silurian; G, *Meristella angustifrons*—Silurian, enlarged; H, Cast of the same. (After Davidson and Hall.)

ranges from the Silurian to the Trias. The shell in this genus (figs. 527, E, and 528) is convex, with unequal valves, the beak of the ventral valve being incurved, and either perforated by a small round foramen, or having the foramen concealed or closed in the adult state. (The *name Athyris*, like that of *Atrypa*, is a zoological misnomer, since in both genera the beak of the ventral valve is really perforated, in the young state at any rate. Some authorities, however, retain the name of *Spirigera* for those forms in which the foramen remains throughout life, and employ that of *Athyris* for those in which this aperture becomes closed in the adult condition, the latter having the additional distinctive character that the interior of the dorsal valve is partially divided by a longitudinal septum.) The spiral supports for the arms in *Athyris* are largely developed, and their pointed extremities are directed towards the lateral angles of the shell (fig. 528, *c*).

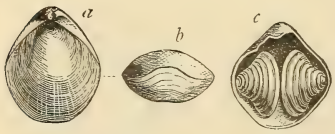

Fig. 528.—*Athyris subtilita*—Lower Carboniferous. The right-hand figure shows the interior of the dorsal valve, with the spiral supports for the arms. (After Dawson.)

Merista (fig. 527, F), of the Silurian and Devonian, is like *Athyris* in general characters, but there is a longitudinal septum in the ventral valve, which is supported by strongly-arched transverse plates, together forming what is known as the "shoe-lifter process." *Meristella* (fig. 527, G and H, and fig. 529) closely resembles the preceding, but the septum and supporting arched plates are wanting in the ventral valve. The genus is

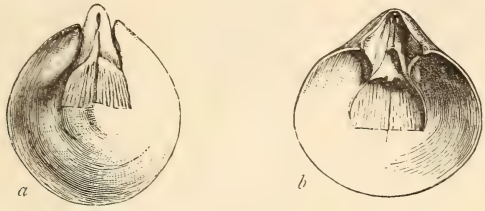

Fig. 529.—*a*, Cast of the interior of the ventral valve of *Meristella nasuta*, from the Devonian (Original); *b*, Interior of the ventral valve of the same (after Billings).

Silurian and Devonian, and a well-known and familiar species is the *Meristella tumida* of the Silurian rocks.

In the Silurian and Devonian genus *Nucleospira*, the shell has a punctated structure, with a short hinge-line, and a false area with a minute peduncular foramen beneath the beak of the ventral valve. There is a low median process in the interior of the ventral valve; and the dorsal

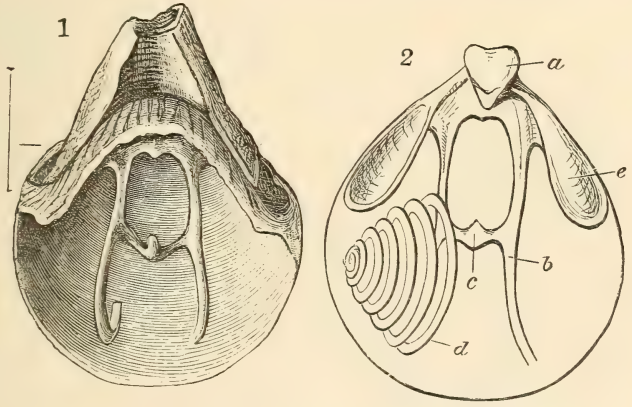

Fig. 530.—1. Interior of a specimen of *Uncites gryphus*, from the Middle Devonian, in which the greater part of the dorsal valve has been removed. The spires are destroyed, but their "crura" remain. 2. Restored interior of the dorsal valve of the same: *a*, Cardinal process; *b*, Principal stems of the spires (*d*); *c*, Band connecting the "crura" of the spires; *e*, Pouch-shaped expansions of the beaks. (After Davidson.)

valve has a spatula-shaped cardinal process, which extends upwards below the beak of the ventral valve, and to the base of which the "crura" of the brachial spires are attached.

The genus *Retzia* includes a large number of species which range from the Silurian to the Trias. The shell in this genus (fig. 527, A) is oval, usually radiately striate or ribbed, the beak of the ventral valve being

perforated by a foramen, below which is a deltidium. The shell-structure is punctated, and the brachial spires are similar to those of *Spirifera*. The names of *Trematospira* and *Rhynchospira* have been proposed for a number of Silurian and Devonian Brachiopods which are closely allied to *Retzia*, but which differ from the typical forms of this genus in some secondary characters.

Lastly, the genus *Uncites* may be placed in this family, though its characters are in some respects peculiar. The valves in *Uncites* (figs. 527, B, and 530) are convex, radially striated, and of an impunctate structure. The beak of the ventral valve is very prominent and strongly curved. The foramen in the beak of the ventral valve disappears early, and there is no true hinge-area, but a large concave deltidium is present, which partially conceals the incurved beak of the dorsal valve. The margins of the beaks are bent inwards, so as to form pouch-shaped expansions external to the hinge. Well-developed brachial processes, of the form characteristic of the *Spiriferidæ*, are present.

The genus *Uncites* is confined to the Devonian rocks, the type being the familiar *U. gryphus* of the Middle Devonian of Europe.

Family 5. Atrypidæ.—In this family the shell-structure is impunctate, and the ventral valve has an incurved beak, with a curved hinge-line and no hinge-area. The essential character of the family, however, is that the dorsal valve is provided with two spirally-coiled brachial supports, the apices of which are directed towards the interior of the valve (fig. 531). The geological range of the family is from the Ordovician to the Trias.

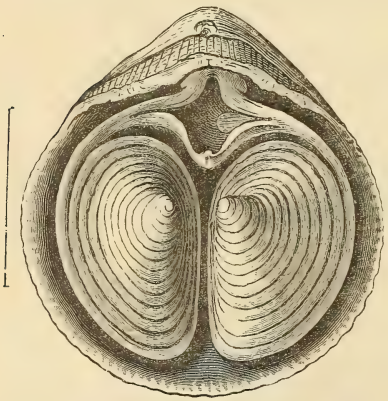

Fig. 531.—*Atrypa reticularis*, from the Silurian rocks of North America, enlarged. The greater part of the dorsal valve has been removed, to show the loop and spiral brachial processes. (After Hall.)

The type of this family is the genus *Atrypa* itself, in which the shell (fig. 532) is biconvex, generally radiately ribbed, and often ornamented with squamose lines of growth. Though named in accordance with the belief that the beak of the ventral valve was imperforate, a small foramen is really present in this genus (fig. 531), sometimes concealed, and sometimes bounded in front by a small deltidium. The spiral brachial processes are large and conical, and are directed with their apices

turned into the hollow of the capacious and ventricose dorsal valve. The species of *Atrypa* range from the Ordovician to the Trias inclusive, an exceedingly familiar and widely distributed species

Fig. 532.—*Atrypa reticularis*. Silurian and Devonian of Europe and America. (After Billings.)

being the *A. reticularis* (fig. 532) of the Silurian and Devonian rocks.

The Silurian and Devonian genus *Cœlospira* is generally regarded as a close ally of *Atrypa*. The brachial supports in this genus are of few coils, and have the peculiarity that the apices of the spires are directed towards each other. The Ordovician and Silurian genus *Zygospira* is also nearly related to *Atrypa*, but the brachial spires have their apices directed obliquely into the cavity of the dorsal valve, and point *towards* each other. On the other hand, in the genus *Dayia* (fig. 533) the spires have their apices turned obliquely into the cavity of the dorsal valve in such a manner as to point *away from* each other, thus facing the sides of the shell. The type of the genus *Dayia* is the familiar Silurian Brachiopod formerly known as *Rhynchonella navicula*, but now termed *Dayia navicula*.

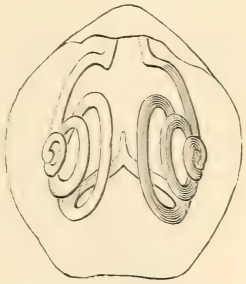

Fig. 533.—Interior of the dorsal valve of *Dayia navicula*, Silurian, enlarged. (After Davidson.)

Family 6. Rhynchonellidæ.—In this family the animal is free, or attached by a muscular peduncle issuing from a foramen beneath the beak of the ventral valve. The arms are spirally coiled, and are supported at their origins only by a pair of short, curved, calcareous processes. The shell-structure is usually fibrous and impunctate, but in a few forms it is tubulated. The shell is biconvex, usually with a curved hinge-line, and a prominent pointed beak in the ventral valve. The geological range of the family is from the Ordovician to the present day, but the great majority of the genera are confined to the Palæozoic rocks.

The type-genus of this family is *Rhynchonella*, in which the valves are more or less convex, smooth, or plaited, and united by teeth and sockets. The shell (fig. 534) is trigonal, generally with a sinus in

the ventral valve and a corresponding fold in the dorsal valve, and having the beak of the ventral valve acute, incurved, and prominent. The foramen is situated beneath the beak, open to view or concealed, and entirely or partially completed by a deltidium. The numerous species of *Rhynchonella* begin in the Ordovician rocks, and the genus is well represented in the Silurian, Devonian, and Carboniferous rocks. In the Secondary series the genus exhibits a

Fig. 534.—*Rhynchonella capax;* dorsal, profile, and ventral views. Ordovician.

marked development in the Jurassic period; but there are few Tertiary species, and only six living forms are known.

The Permian Brachiopods which have been included under the name of *Rhynchoporina* resemble *Rhynchonella* in all essential respects, but the shell is punctated. In the Silurian genus *Eatonia*, hitherto only found in North America, the teeth in the ventral valve are prolonged into elevated ridges which enclose the muscular impressions, these latter being divided by a median septum, a more developed septum being present in the dorsal valve as well. In the Triassic genus *Dimerella*, again, there is a large triangular foramen beneath the beak of the ventral valve, and the dorsal valve has a prominent median septum which divides the umbonal half of the cavity of the shell into two chambers. In *Leio-*

Fig. 535.—*Leiorhynchus Huronensis*, viewed dorsally (*a*), ventrally (*b*), and in profile (*c*). Devonian. (Original.)

rhynchus (fig. 535) are various Devonian Brachiopods, very closely allied to *Rhynchonella* proper, but having the plications of the shell obsolete on the lateral angles, while well marked on the mesial fold and sinus. The beak of the ventral valve is pierced by a foramen, in at any rate the early stages of growth, and there is a well-defined septum in the dorsal valve. *Triplesia* (Silurian) has a triangular pedicle-notch beneath the beak of the ventral valve, the hinge-line being straight, with a well-defined hinge-area; while the cardinal process in the dorsal valve is prominent and bifurcated, and the shell itself is trilobate. In the Ordovician

genus *Camarella* the shell is almost equivalve, the ventral valve having an incurved imperforate beak; and the dental lamellæ converge to form beneath the beak of the ventral valve a small triangular chamber, from which a median septum is continued. A similar median septum is continued in the dorsal valve from the bases of the brachial processes. Lastly, the genus *Stenoschisma* (=*Camarophoria*, King) possesses a shell like that of *Rhynchonella*, but the teeth in the ventral valve are supported by converging lamellæ, which unite to form a low median septum, while a more pronounced septum is developed in the interior of the dorsal valve. The species of this genus are abundant in the Devonian rocks of North America, while other species occur in the Carboniferous and Permian rocks.

Fig. 536.—*Stenoschisma* (*Camarophoria*) *globulina*. Permian. (After King.)

All the preceding forms are naturally associated with one another by their structural characters; but there is another great group of Brachiopods usually placed in the *Rhynchonellidæ*, and agreeing with this family in many points, of which the genus *Pentamerus* is the type, and which presents certain distinctive features of its own. In *Pentamerus* (fig. 537) the shell is ovate, the valves articulated by teeth and sockets, and the surface generally ribbed or striated, but sometimes smooth. The beaks are incurved, that of the ventral valve concealing a triangular fissure. Inside the ventral valve "two contiguous vertical septa coalesce into one median plate, extending

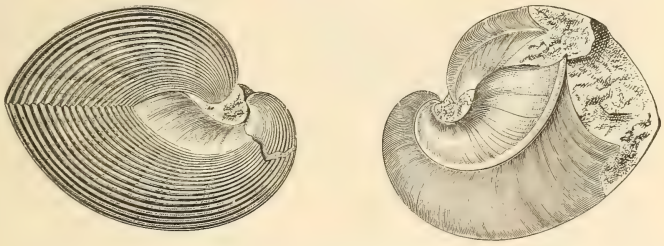

Fig. 537.—*Pentamerus Knightii*. The right-hand figure shows the internal septa and dental plates of the shell. Silurian.

from the beak to a greater or less distance; and then diverge and form the dental plates, enclosing a triangular chamber of much smaller dimensions than the lateral ones" (Davidson). The small central chamber must have been occupied by the digestive organs, and the spiral arms must have filled the great lateral spaces. In the interior of the smaller or dorsal valve are two longitudinal septa, which often form a chamber corresponding with and apposed to the median chamber in the ventral valve. The *Pentameri* are confined to the Silurian and Devonian deposits, particular species being often

restricted to definite horizons, while some forms have a very wide geographical range. Well-known Silurian species are *P. Knightii*, *P. oblongus* (fig. 538), and *P. undatus*, while *P. globus* and *P. acutolobatus* are Devonian, and the familiar *P. galeatus* is found in both sets of deposits.

In the typical forms of *Pentamerus* the shell is more or less globose, the ventral valve is much the largest, and the median septum in the same valve is very long. In certain Silurian species, however, which have been placed in *Pentamerus*, and for which Mr Billings proposed the name of *Stricklandia* (=*Stricklandinia*), the two valves (fig. 539) are

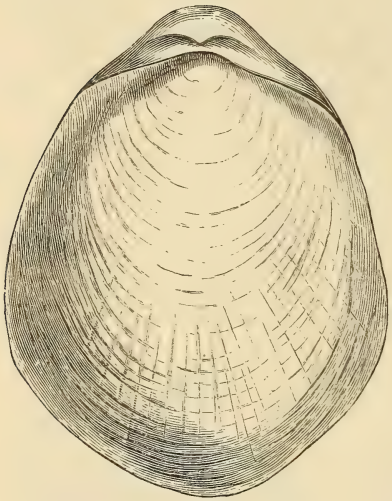

Fig. 538.—Large specimen of *Pentamerus oblongus*. Silurian. (Original.)

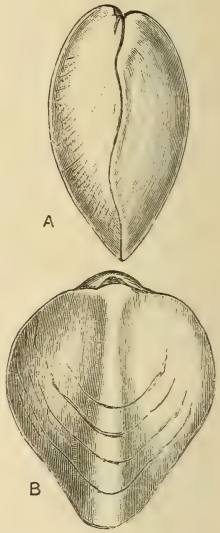

Fig. 539. — *Stricklandia Davidsoni*, viewed sideways and dorsally. Silurian. (After Billings.)

not very disproportionately unequal, the shell is often more or less depressed, and in the ventral valve there is but a short mesial septum which supports a V-shaped chamber beneath the beak ; whereas in the dorsal valve there are only two short socket-plates. *Pentamerella*, *Amphigenia*, *Gypidula*, and *Anastrophia* are other generic or sub-generic titles which have been proposed for forms more or less closely allied to *Pentamerus* itself. The first three of these occur in the Devonian, but the last is found in the Silurian deposits of North America.

The genus *Porambonites* occupies a doubtful position, being sometimes placed in the present family, and sometimes referred to the *Strophomenidæ*. In this genus the shell is globose and almost equivalve, with a mesial fold and sinus in front ; and the beak of the ventral valve has a small foramen. The hinge-teeth in the ventral valve are supported by strong dental lamellæ, which unite to form a small median septum.

The surface is apparently smooth, but is in reality ornamented with minute, close-set circular pits disposed in radiating lines. The species of *Porambonites* are characteristic of the Ordovician rocks, and are especially abundant in deposits of this age in the Baltic provinces of Russia.

Family 7. Terebratulidæ.—The shell in the *Terebratulidæ* is minutely punctate in structure, and is rounded or oval in form, the

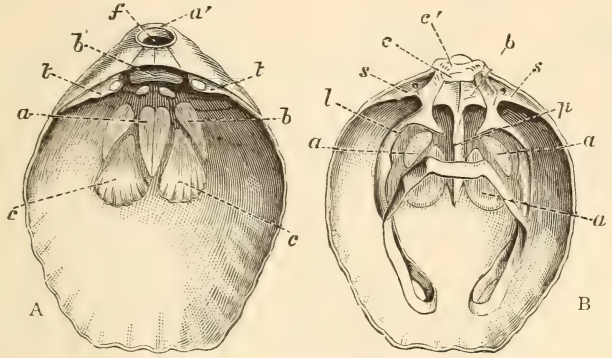

Fig. 540.—Interior of the ventral valve (A) and dorsal valve (B) of the recent *Waldheimia flavescens*. *a'*, Beak of the ventral valve with the foramen (*f*); *t*, Hinge-teeth; *p*, Septum of dorsal valve; *l*, Brachial loop; *s*, Dental sockets; *a a*, Adductor-impressions; *b b*, Ventral adjustors; *c c*, Divaricator-impressions; *b'*, Peduncular muscles; *c'*, Cardinal process. (After Davidson.)

surface being smooth or striated. The beak of the ventral valve (fig. 540, *a'*) is prominent, and is perforated by a foramen, through which passes the peduncle of attachment, and which is partially surrounded by a deltidium of one or two pieces. The arms are supported by a loop-shaped brachial process (fig. 540, *l*), which

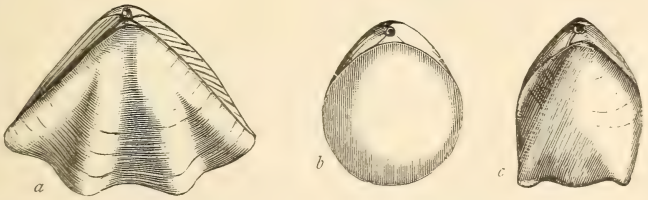

Fig. 541.—*a*, *Terebratula quadrifida*—Lias; *b*, *Terebratula sphæroidalis*—Inferior Oolite; *c*, *Terebratula digona*—Bradford Clay, Forest Marble, and Great Oolite (Jurassic). (After Davidson.)

varies in length and form in different types of the family, and which springs from the hinge of the dorsal valve. As regards its geological range, the family of the *Terebratulidæ* is represented in deposits as old as the Devonian, or even the Silurian; but it attains its maximum development in the Mesozoic and Kainozoic deposits,

and it is represented at the present day by a number of living forms.

In the genus *Terebratula* itself, as now usually restricted, the shell (fig. 541) is oval or circular, with a smooth surface, and either simply rounded in front, or exhibiting a mesial fold in the ventral valve, to which corresponds a sinus, with a lateral fold on each side, in the dorsal valve. The beak of the ventral valve is short, with a wide foramen, below which is a deltidium. The brachial loop (fig. 542) is short, and does not extend to more than a third of the distance between the hinge-line and the anterior margin of the shell. The oldest forms of the *Terebratulæ* appear in the Devonian, and other forms are found in the Carboniferous and Permian deposits. These early examples of the genus differ from later types in the possession of strong dental supports beneath the hinge of the ventral valve. Throughout the Secondary rocks, and especially in the Jurassic and Cretaceous formations, the genus is largely represented, while there is also a limited number of Tertiary types, and several living species are known.

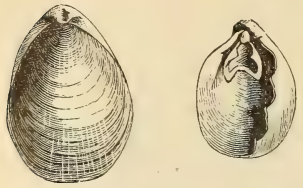

Fig. 542.—*Terebratula sacculus*—Carboniferous. The right-hand figure shows the interior of the dorsal valve with the loop. (After Dawson.)

In *Terebratulina* (fig. 543) the exterior of the shell is ornamented with dichotomous radial striæ, and the brachial loop is very short, and is converted into a simple ring. The species of *Terebratulina* range from the Jurassic to the present day.

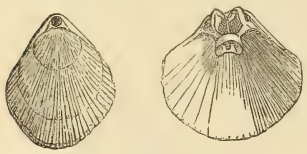

Fig. 543.—*Terebratulina substriata*, Upper Jurassic, of the natural size. (After Zittel.)

The genus *Waldheimia* is the type of another series of the *Terebratulidæ*, in which the brachial loop is elongated, its length equalling at least half that of the shell itself (fig. 540). In addition to the presence of a long brachial loop, another distinctive character of *Waldheimia* is the existence of a more or less developed median septum in the interior of the dorsal valve. The species of *Waldheimia* appear to commence in the Lias, and the genus is well represented at the present day. There are no dental plates in the ventral valve of *Waldheimia*, but such plates are developed in the closely allied *Zeilleria* of the Jurassic, Cretaceous, and older Tertiary formations.

In the Silurian, Devonian, and Carboniferous genus *Centronella* (fig. 544), the shell has the general characters of *Terebratula*, but the brachial loop consists of two delicate ribbon-like lamellæ, which extend about one-half the length of the shell. "These lamellæ at first curve gently outwards, and then approach each other gradually, until at their lower extremities they meet at an acute angle; then, becoming united, they are reflected backwards towards the beak, in what appears to be a thin, flat, vertical plate. Near their origin each bears upon the ventral side

a single triangular crural process" (Billings). The species of this genus seem to be mainly confined to the Palæozoic rocks of North America; but European forms are known. The Silurian and Devonian genus *Leptocœlia* seems to be nearly allied to *Centronella*, but the shell is radiately-ribbed, whereas in the latter genus it is smooth. The Silurian and Devonian genera *Rensselæria* and *Meganteris* likewise include ancient types of the *Terebratulidæ*.

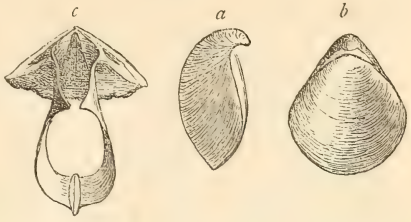

Fig. 544.—Lateral (*a*) and dorsal (*b*) views of *Centronella glans-fagea*, from the Devonian rocks of North America, of the natural size; *c*, Brachial loop of the same, enlarged. (After Hall—copied from Zittel.)

In the genus *Terebratella* (fig. 545) the shell is sometimes smooth, sometimes radiately-ribbed, and there is an incomplete deltidium (*m*) below the foramen. In the dorsal valve is a well-developed mesial septum, with which the brachial loop becomes secondarily connected by means of transverse calcareous processes, one on each side. The genus *Terebratella* begins in the Lias, is well represented in the Cretaceous formation, and still exists at the present day.

Various Mesozoic, Tertiary, and Recent Brachiopods are closely re-

Fig. 545.—*Terebratella Astieriana*—Cretaceous. *e*, Hinge-area; *m*, Deltidium.

lated to *Terebratella*, with which they agree in the fact that the brachial loop, in addition to its normal attachment to the hinge-line, has a secondary connection with a median septum in the dorsal valve. Among the forms in question, *Lyra* (*Terebrirostra*) has a greatly elongated beak to the ventral valve, and is confined to the Cretaceous period. The genus *Trigonosemus*, also Cretaceous, has an incurved beak, a large cardinal process, and an extensive hinge-area. In the genus *Magas*, of the Cretaceous period, the dorsal septum is so greatly developed as almost to divide the cavity of the shell into two halves; while in *Megerlia* (Chalk to Recent) the brachial loop is not only attached to the hinge-plate, but is doubly connected with the dorsal septum. The Jurassic and Cretaceous *Kingena*, and the recent *Bouchardia* and *Kraussina* are other types belonging to the same group.

Family 8. Argiopidæ.—In this family there is a large foramen for the transmission of the peduncle of attachment, and the dorsal

valve is provided with one or more sub-marginal septa, with which the brachial loop becomes more or less extensively fused. The shell-structure is punctate. The range of the family is from the Jurassic period to the present day.

The type-genus of this family is *Argiope* itself, which ranges from the Upper Jurassic to the present day. In this genus the shell (fig. 546) is transversely oval, with a straight hinge-line and an area to each valve, and having a large foramen, with a rudimentary deltidium. The interior of the dorsal valve is furnished with from three to five sub-marginal septa (*s*); while the brachial loop follows the margin of the shell, and becomes attached to the septa, thus becoming four-lobed, being at the same time partially confluent with the shell. *Cistella* (Lias to Recent) closely resembles *Argiope* in general characters, but there is only a single septum in the dorsal valve, and the brachial loop is two-lobed.

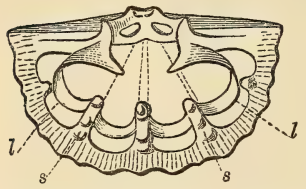

Fig. 546.—Interior of the dorsal valve of *Argiope decollata* (Recent), enlarged, showing the sub-marginal septa (*s*) and the brachial loop (*l*). (After Davidson.)

Family 9. Stringocephalidæ.—In this family the shell is rounded; the beak of the ventral valve possesses a foramen and

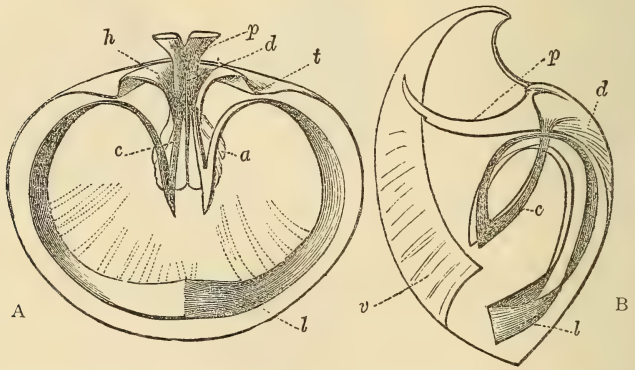

Fig. 547.—A, Interior of the dorsal valve of *Stringocephalus Burtini*, Middle Devonian; B, Shell of the same viewed in profile and showing the interior: *a*, Adductor impression; *p*, Cardinal process; *h*, Hinge-plate; *c*, Crura of loop (*l*); *d*, Dorsal septum; *v*, Ventral septum; *t*, Dental sockets. The radial processes of the loop are shown in A by dotted lines. (After Davidson.)

deltidium; the cardinal process of the dorsal valve is greatly developed; and the brachial loop is marginal, and carries internally-directed radial processes. The only genus comprised in this family is *Stringocephalus* itself, which is confined to the Silurian and Devonian rocks.

The type-species of *Stringocephalus* is the well-known *S. Burtini* of the Middle Devonian of Europe. In this well-known species (figs. 547 and 548) the shell is sub-orbicular, with a prominent beak to the ventral valve, and often growing to a great size. There is a large foramen below the beak of the ventral valve, which is triangular in the young shell, but ultimately becomes oval and reduced in size by the growth of the deltidium. The ventral valve has prominent teeth, fitting into corresponding sockets (*t*) in the dorsal valve. The cardinal process (*p*) in the dorsal valve is very prominent, and its free end is bifurcated to receive a well-developed median septum (*v*) in the ventral valve. A corresponding, but much smaller septum (*d*) is present in the dorsal valve. The hinge-plate (*h*) of the dorsal valve gives origin to a large brachial loop (*l*), consisting of two crura (*c*) which are reflected backwards about the middle of the valve, and then, bending forwards, give origin to a wide ribbon-

Fig. 548.—*Stringocephalus Burtini*—Devonian—reduced in size.

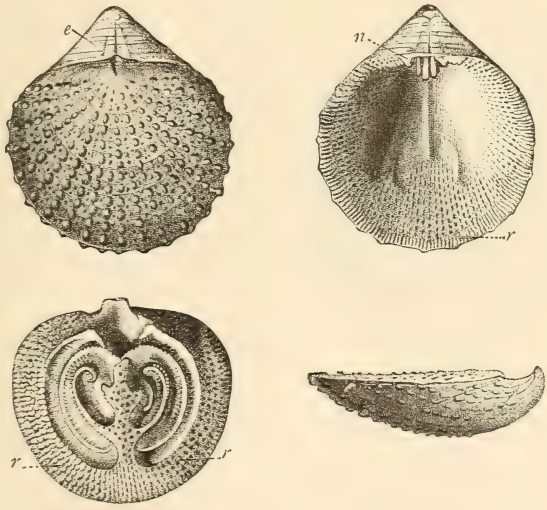

Fig. 549.—*Thecidium papillatum*. *e*, Hinge-area; *n*, Hinge-teeth of ventral valve *r r*, Granulated border of the interior of the dorsal valve. Cretaceous.

shaped band, which is sub-marginal in position, and gives off radiating shelly processes along its inner margin.

Family 10. Thecidiidæ.—In this family the shell is usually fixed to the sea-bottom by the substance of the beak of the ventral valve; the arms are united in the form of a bridge over the visceral

cavity, are folded upon themselves, and are supported by a calcareous loop; and the mantle is strengthened by a copious development of calcareous spicula. The inner layer of the shell is fibrous, but the outer layer is tubulated. The geological range of the family is from the Carboniferous to the present day.

The type-genus of this family is *Thecidium* (= *Thecidea*) which commences in the Upper Trias, is well represented in parts of the Jurassic and Cretaceous rocks, and survives under two specific forms at the present day. In this genus the shell (fig. 549) is plano-convex, and is fixed by the substance of the beak of the ventral valve, or may be free in the adult condition. The hinge-line is straight, with powerful hinge-teeth in the ventral valve, this valve being further distinguished by the presence of a large triangular hinge-area, in which is a pseudo-deltidium. The margins of both valves exhibit internally a broad granulated and thickened border. In the dorsal valve is a prominent cardinal process, flanked by the dental sockets, below which the brachial supports unite to form a slender bridge. The loop follows the margin of the shell, generally forming more or fewer lobes, and is either confluent with the shell, or is connected with a calcareous network formed by the largely developed spicula in the mantle.

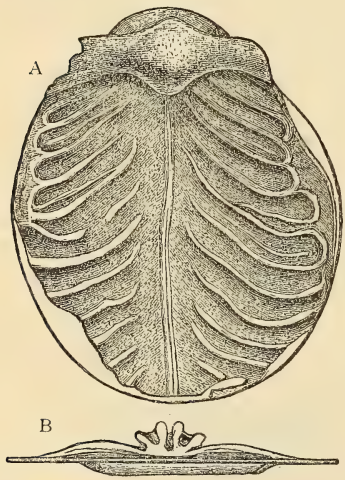

Fig. 550.—A, Interior of the ventral valve of *Oldhamina decipiens*, from the Carboniferous rocks of India; B, Cardinal view of the dorsal valve. (After Waagen.)

Besides the Liassic types included under the names of *Eudesella*, *Davidsonella*, and *Bactrynium*, this family includes the remarkable Carboniferous types described by Waagen under the names of *Oldhamina* and *Lyttonia*. In these singular forms the shell is of large size, flat or gibbous, and attached by the ventral valve. The hinge-line is straight and short, without an area or pseudo-deltidium. Internally, the ventral valve exhibits a median septum, flanked on both sides by numerous, transverse and oblique, lateral septal ridges. The dorsal valve is rudimentary, "forming together with the brachial apparatus one strongly-lobed shelly plate, which fits between the external septa of the large valve" (Waagen). These abnormal types have hitherto been detected only in the Carboniferous rocks of India, and they are regarded by Waagen as forming a special sub-family of the *Thecidiidæ*.

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CHAPTER XXXV.

SUB-KINGDOM MOLLUSCA.

GENERAL CHARACTERS OF THE MOLLUSCA—GENERAL CHARACTERS OF THE LAMELLIBRANCHIATA.

THE *Mollusca* may be defined as *soft-bodied, bilaterally symmetrical, not definitely segmented animals. The anterior part of the body is very generally developed into a distinct head, bearing one or more pairs of soft tactile processes or tentacles. The mouth is anterior, the alimentary canal is completely shut off from the general cavity of the body, and the anus is primitively posterior. The nervous system consists of a small number of paired ganglia. A distinct vascular system and a systemic heart are present. One or more pairs of kidneys (sometimes a single kidney) are present as saccular organs ("nephridia"), which open internally into the body-cavity, and communicate with the exterior by a pore placed near the anus. Commonly there is an external or internal "shell."*

The body of a Mollusc exhibits a distinct dorsal and ventral surface, and a right and left side. The dorsal surface is covered by a fold of the integument which constitutes what is called the "mantle" or "pallium," and which may be greatly expanded laterally, or may form a complete sac enclosing all the viscera. The so-called "mantle-cavity" or "pallial chamber" is the space included between the lateral prolongations of the mantle and the sides of the body.

From the ventral side of the body there is, typically, developed an unpaired median muscular mass, which constitutes what is called the "foot." The foot (fig. 551, *f*) may show a distinct division into an anterior, a middle, and a posterior region; and it is often furnished with distinct lateral prolongations ("epipodia"). The foot undergoes remarkable modifications in different groups of the *Mollusca*.

The alimentary canal commences at the mouth (fig. 551, *m*),

which may or may not be provided with an apparatus of teeth, or may be furnished with tactile processes. The digestive tube is commonly of considerable length, and usually shows a gullet, into which salivary glands pour their secretion, a stomach, and an intestine. The rectum terminates at the anal aperture (fig. 551, *a*), which is primitively at the hinder end of the body, but which in many forms ultimately becomes shifted further forward. The blood is colourless; and a definite heart, consisting of a ventricle and one or two

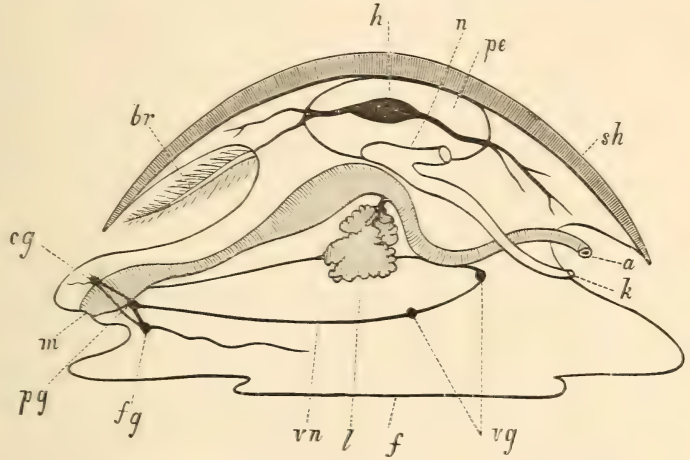


Fig. 551.—Diagram of a Mollusc (altered from Lankester). *m*, Mouth; *a*, Anus; *l*, Liver; *f*, Foot; *sh*, Shell, attached to the mantle; *h*, Heart; *pe*, Pericardium; *n*, Kidney, opening internally into the pericardium, and externally near the anus (*k*); *br*, Gill; *cg*. One of the cerebral ganglia, connected by commissures with the pleural ganglion (*pg*) and the pedal ganglion (*fg*); *vn*, Visceral nerve-cord extending backward, and carrying visceral ganglia (*vg*).

auricles, is always present, and always has the function of propelling the aerated blood through the body.

Respiratory organs are not always developed, the function of respiration being in some cases discharged by the thin walls of the mantle-cavity. In the majority of the Molluscs, however, there are definite respiratory organs, a portion of the mantle being specialised for this purpose. In the *Lamellibranchiata*, and the branchiate *Gastropoda*, the breathing-organs are in the form of lamellar or pectinate gills; and the same is the case with the *Cephalopoda*. In the pulmonate *Gastropoda*, in which respiration is aerial, a pulmonary sac or air-chamber is produced by the folding of a portion of the mantle, over the interior of which the pulmonary vessels are distributed, and the external opening of which is placed on the side of the neck.

The nervous system consists of paired ganglia united by com-

missures. The most important ganglia are (1) a pair of "cerebral" ganglia, placed above the gullet; (2) a pair of "pedal" ganglia placed below the gullet, and supplying the foot and adjacent parts; and (3) a group of "visceral" ganglia placed towards the posterior part of the body.

Reproductive organs are always present, and the sexes may be distinct or united. There is usually a well-marked metamorphosis in development, and the embryo very commonly passes through a "trochosphere" stage, in which it swims about actively by means of a circlet of cilia placed in front of the mouth, and closely resembles the larva of many Annelides. The young Mollusc possesses a glandular involution of the dorsal integument, which produces an embryonic shell, and this may either be cast off as development proceeds, or may remain permanently as part of the shell of the adult. In the Spiral Gastropods the embryonic shell or "nucleus" is placed at the apex of the permanent shell, whereas in the Bivalves it is situated at the beak or "umbo."

The Molluscs very generally develop an integumentary skeleton in the form of a "shell," which in all forms, except in the Argonaut, is secreted by the mantle. In chemical composition the shell consists of carbonate of lime disseminated throughout an organic matrix. The atomic arrangement of the carbonate of lime differs in different cases, some Molluscs having the shell wholly composed of calcite, while in others it is wholly composed of aragonite, and in many forms it consists of an inner layer of aragonite and an outer layer of calcite. Very generally the outer surface of the shell is covered by an easily recognisable horny external layer (the "epidermis" or "periostracum"), but this may be exceedingly thin, or may disappear altogether in the course of growth. Some of the more important points in the microscopic structure of the shell will be briefly noticed in dealing with the different groups of Molluscs. While the presence of a shell is very characteristic of the Molluscs, there are many so-called "naked" forms, in which the adult is either totally devoid of a shell, or possesses only a rudimentary shell enclosed in the substance of the mantle.

The *Mollusca* may be roughly divided into two great sections, respectively termed the *Acephala* and the *Encephala* (or *Cephalophora*), characterised by the absence or presence of a distinctly differentiated head. The headless, or Acephalous, Molluscs correspond to the class *Lamellibranchiata;* also distinguished, at first sight, by the possession of a bivalve shell. The Encephalous Molluscs are more highly organised, and are divided into the two principal classes of the *Gastropoda* (including the *Pteropoda*) and the *Cephalopoda*, with which may be associated the two small and aberrant groups of the *Polyplacophora* (Chitons) and *Scaphopoda*

(Tooth-shells). The shell in the Encephalous Molluscs is of a very different nature in different cases, but all the members of this section possess a complicated series of lingual teeth, and they have for this reason been grouped together by Professor Huxley under the name of *Odontophora*.

As regards their *distribution in space*, all the members of the *Mollusca* are aquatic in their habits with the exception of a portion of the Pulmonate Gastropods, many of these, however, being inhabitants of water, though others are strictly terrestrial. The water-inhabiting Molluscs may live in the sea, or in brackish or fresh waters. Owing to their generally living in water, and owing also to their so commonly possessing hard structures, whether external or internal, no fossils are more abundant or more important than the remains of the *Mollusca*. As regards the general *distribution in time* of the Molluscs, all the principal classes (viz., the *Lamellibranchiata*, *Gastropoda*, and *Cephalopoda*) are represented in the Upper Cambrian deposits, and it is therefore clear that we have at present no knowledge of the really primordial types of the sub-kingdom. Speaking generally, the chief representatives of the *Mollusca* in Palæozoic time are the chambered Cephalopods (*Tetrabranchiata*), the Dibranchiate Cephalopods apparently not having come into existence, while the Lamellibranchs and Gastropods show a comparatively limited development. In Mesozoic time, the Dibranchiate Cephalopods make their first appearance, and undergo a vast development, while the Tetrabranchiate division of this class has also a wonderful representation. The Lamellibranchs are very largely represented in the Mesozoic deposits, but the Gastropods still play a subordinate part. In Kainozoic time, on the other hand, the Cephalopods undergo an extraordinary reduction, the group of the Tetrabranchiates becoming almost extinct, while the Lamellibranchs and Gastropods, the latter particularly, assume a predominant position. At the present day, the Lamellibranchs and Gastropods are the two leading classes of Molluscs, and both seem to have attained their culminating point in existing seas.

Class I. Lamellibranchiata.

The *Lamellibranchiata* (= *Conchifera* or *Pelecypoda*) are often familiarly spoken of as the "Bivalve Molluscs," and are characterised by *the absence of a distinctly differentiated head, and by having the mantle divided into two lobes, right and left, each of which secretes a shelly investment, so that the body is more or less completely enclosed in a bivalve shell. There are one or two pairs of lamellar gills on each side of the body. An odontophore is wanting. The sexes are distinct or united.*

The body in the Lamellibranchs is bilaterally symmetrical, and is enclosed in a largely developed "mantle" or "pallium," which is divided into two lateral halves, the right and left "lobes" of the mantle. The two lobes of the mantle are united along the dorsal side of the body, and are prolonged laterally as two great flaps, which conceal the body, and enclose inferiorly a chamber known as the "mantle-cavity." The lower or ventral edges of the mantle-lobes are normally free; but in many Bivalves they become more or less fused with one another (fig. 552), so that the animal is enclosed in a complete sac, in which certain openings are left anteriorly and posteriorly. Two of these apertures are at the posterior end of the animal, and serve to permit the ingress into the mantle-cavity of the water required for respiration and for the purpose of obtaining food, and the egress of the same. The lower or ventral aperture is inhalant in function; the upper or dorsal aperture is exhalant; and the anus is always placed in the vicinity of the latter, so that excrementitious matters are carried away in the outgoing currents of water. In many cases these two openings into the mantle-sac are drawn out into longer or shorter muscular tubes, which are known as the "siphons." In those Bivalves which have the ventral margins of the mantle-lobes *free*, the in-going and outgoing currents of water still enter and leave the mantle-cavity by openings at its posterior end.

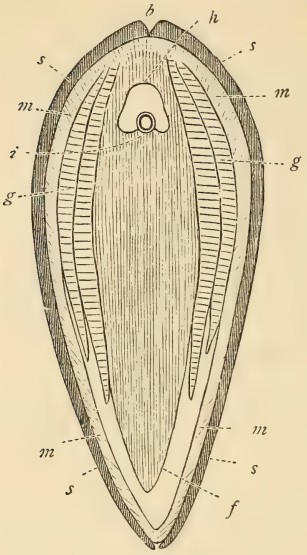


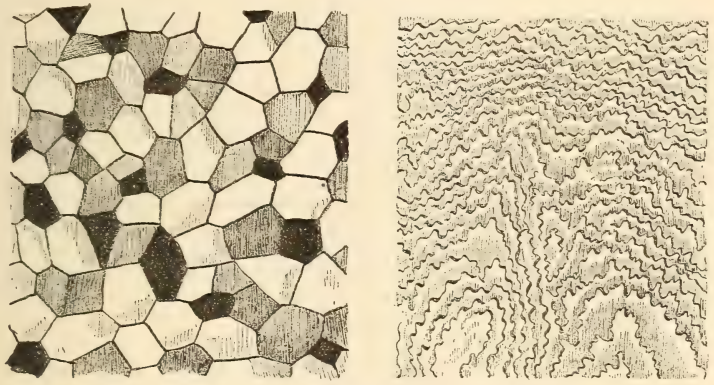
Fig. 552.—Diagrammatic vertical and transverse section of *Mya arenaria*. *b*, Back, or "dorsal margin" of the shell; *s s*, The two valves of the shell, right and left; *m m*, The two halves, or "lobes," of the mantle, producing the shell; *g g*, The gills, two pairs on each side; *h*, The heart; *i*, Intestine; *f*, The foot.

In those Bivalves which have the mantle-lobes fused along their ventral edges, a third aperture is necessary in order to allow of the protrusion of the "foot." This aperture is always placed ventrally and towards the anterior end of the animal. In the forms with free mantle-lobes no special opening is needed for the protrusion of this organ.

The "foot" of the Bivalves is not so extensively developed as in the Gastropods. Usually it forms a hatchet-shaped muscular organ, which may be used in locomotion, but is hardly ever adapted for crawling. In other cases it is cylindrical in shape, and in the

sedentary Bivalves it is more or less completely aborted. In many cases, especially in the young, there is developed, on the under surface of the foot, in the middle line, a peculiar "byssal gland." This gland secretes a viscid material which is moulded into threads by grooves on the external surface of the foot, and which gives rise to a tuft of silky fibres (the "byssus"), serving to moor the animal to foreign objects, and often having a special notch or aperture in the shell for its emission.

The *shell* of the Bivalves is the result of the deposition of lime-salts in the outer layer of the mantle, chiefly along its ventral margins; and as the mantle is divided into a right and left "lobe," so the shell also is divided into a right and left "valve." The outer surface of the shell is usually covered by thinner or thicker horny "epidermis" or cuticle, but this may become obsolete in the adult. The calcareous tissue of the shell itself is very generally disposed in two distinct strata, of which the outer is prismatic, and the inner is



A B

Fig. 553.—A, External surface of *Pinna*, showing the ends of the prisms of the outer shell-layer, greatly enlarged; B, Polished surface of mother-of-pearl, enlarged eighty-five times. (After W. B. Carpenter.)

laminated. The outer prismatic layer is secreted by the free edges of the mantle-lobes, and grows, therefore, at the circumference of the shell only. It consists, in the majority of cases, of polygonal calcareous prisms, placed side by side in close contact, and directed perpendicularly to the surface of the shell. Hence sections of this layer taken parallel with the surface exhibit the transversely-divided prisms as a pavement of hexagonal or polygonal cells; and the same appearance is seen on examining the surface of this layer under a sufficient magnifying power (fig. 553, A). The prisms of the outer layer of the shell vary considerably in diameter, length, regularity, and precise mode of arrangement in different Bivalves. The inner

layer of the shell is laminated, and is secreted by the whole outer surface of the mantle. Hence, this stratum is produced in successive layers throughout the entire life of the animal, each new layer extending a little beyond the one last formed; and in this way are produced the concentric "lines of growth," which are so characteristic of the shells of the Bivalves. The calcareous laminæ composing the inner layer of the shell are disposed approximately parallel to the surface. In many cases (fig. 553, B) the laminæ are very delicate, and are more or less crumpled or undulated, so that when the minute undulations of the successive layers of this stratum are exposed on the surface, the rays of light are broken up in such a way as to give rise to the iridescence and play of colours characteristic of "mother-of-pearl" or "nacre." In other cases, however, the laminæ of this internal stratum are thicker, and are not minutely undulated, and this layer then assumes a "porcellanous" character.

As regards the chemical composition of the shell in the Bivalves, considerable differences obtain as to the precise condition in which the carbonate of lime presents itself. In some cases (as, for example, in *Ostrea*), both the outer and inner layers of the shell are composed of calcite, whereas in others both layers are formed of aragonite. In other cases, again (as in *Pinna*), the outer prismatic layer is composed of calcite, while the inner laminated layer is formed of aragonite. Owing to the greater destructibility and instability of aragonite as compared with calcite, these differences in composition lead to considerable differences in the mode of preservation of different types of the Bivalves. Thus, forms in which the shell is wholly composed of aragonite are often represented in the fossil state solely by moulds and casts; while in those in which the two layers of the shell differ in composition, the inner aragonite-layer of the shell may have been wholly removed, while the outer calcite-layer may be well preserved.

Though the Bivalves agree with the *Brachiopoda* in possessing a shell which is composed of two pieces or valves (small accessory plates are present in *Pholas*, &c.), there are, nevertheless, many points in which the shell of a Lamellibranch is distinguished from that of a Brachiopod, irrespective of the great difference in the structure of the animal in each. The shell in the *Brachiopoda*, as we have seen, is rarely or never quite equivalve, and always has its two sides equally developed (equilateral); whilst the valves are placed antero-posteriorly as regards the animal, one in front and one behind, so that they are "dorsal" and "ventral." In the *Lamellibranchiata*, on the other hand, the two valves are usually of nearly equal size (equivalve), and are more developed on one side than on the other (inequilateral); whilst their position as regards the animal is always *lateral*, so that they are properly termed "right" and "left" valves, instead of "ventral" and "dorsal."

It is to be remembered, however, that many of the Bivalves, such as the Oysters, habitually lie on one side, in which case the valves, though really right and left, are called "upper" and "lower." It is to be borne in mind, also, that the two valves, especially in the attached Bivalves, may be very unsymmetrical, one valve being much larger or deeper than the other. Lastly, there are some cases (*e.g.*, *Pectunculus*) in which the shell becomes very nearly equilateral, the line drawn from the beaks to the base dividing the shell into two almost equal halves.

The following are the chief points to be noticed in connection with the shell of any Lamellibranch (fig. 554): Each valve of the shell may be regarded as essentially a hollow cone, the apex of which is turned more or less to one side; so that more of the shell is situated on one side of the apex than on the other. The apex of the valve is called the "umbo," or "beak," and is mostly turned towards the mouth of the animal. Consequently, the side of the

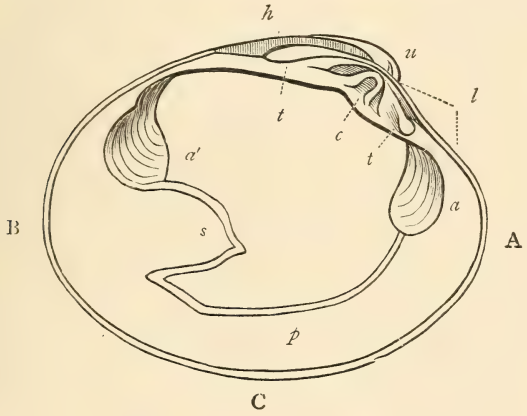


Fig. 554.—Left valve of *Cytherea chione*. (After Woodward.) A, Anterior margin; B, Posterior margin; C, Ventral margin or base. *u*, Umbo; *h*, Ligament; *l*, Lunule; *c*, Cardinal tooth; *t t*, Lateral teeth; *a*, Anterior adductor; *a'*, Posterior adductor; *p*, Pallial line; *s*, Pallial sinus, caused by the retractor muscles of the siphons.

shell towards which the umbones are turned is the "anterior" side, and it is usually the shortest half of the shell. In some Bivalves, however, the beaks are "reversed," and are turned towards the posterior side of the shell. The longer half of the shell, from which the umbones turn away, is called the "posterior" side, but in some cases this is equal to, or even shorter than, the anterior side. The side of the shell where the beaks are situated, and where the valves are united to one another, is called the "dorsal" side; and the opposite margin, along which the shell opens, is called the "ventral"

side or "base." The *length* of the shell is measured from its anterior to its posterior margin, and its *breadth* from the dorsal margin to the base.

At the dorsal margin the valves are united to one another, for a shorter or longer distance, along a line which is called the "hinge-line." The union is effected in most shells by means of a series of parts which interlock with one another (the "teeth"), but these are sometimes absent, when the shell is said to be "edentulous." Posterior to the umbones, in most Bivalves, is another structure passing between the valves, which is called the "ligament," and which is usually composed of two parts, either distinct or combined with one another. These two parts are known as the "external ligament" (or the ligament proper) and the "cartilage," and they constitute the agency whereby the shell is opened; but one or other of them may be absent. The ligament proper is outside the shell, and consists of a band of horny fibres, passing from one valve to the other just *behind* the beaks, in such a manner that it is put upon the stretch when the shell is closed. The cartilage, or internal ligament, is lodged between the hinge-lines of the two valves, generally in one or more "pits," or in special processes of the shell. It consists of elastic fibres placed perpendicularly between the surfaces by which it is contained, so that they are necessarily shortened and compressed when the valves are shut. To open the shell, therefore, it is simply necessary for the animal to relax the muscles which are provided for the closure of the valves, whereupon the elastic force of the ligament and cartilage is sufficient of itself to open the shell.

Generally the hinge-line is curved, but it is sometimes straight. The beaks are mostly more or less closely contiguous; but they may be removed from one another to a greater or less distance, and in some anomalous forms they are not near one another at all. In the genus *Arca* the two beaks are separated from one another by an oval or lozenge-shaped flat space or area. When teeth are present, they differ much in their form and arrangement. In many forms (fig. 554) the teeth are divisible into three sets—one group, of one or more teeth, placed immediately beneath the umbo, and known as the "cardinal teeth"; and two groups on either side of the preceding, termed the "lateral teeth." Sometimes there may be lateral teeth only; sometimes the cardinal teeth alone are present; and in some cases (*Arcidæ*) there is a row of similar and equal teeth.

While the opening of the valves of the shell of a Lamellibranch is effected by the elastic force of the ligament, the closure of the valves is effected by the contraction of one or two powerful muscles, which are known as the "adductor muscles." In the majority of Bivalves—hence termed *Dimyaria*—there are two adductor muscles,

which pass from the inner surface of one valve to that of the other, one being placed anteriorly in front of the mouth, while the other is situated posteriorly close to the termination of the intestine (fig. 555, *a* and *a'*). Moreover, among the Dimyary Bivalves the adductors present two markedly different conditions. In one group of forms — hence termed *Homomyaria*—the anterior and posterior adductors are approximately equal in size. In a second series—hence termed *Heteromyaria* — the anterior adductor is very small, and the posterior adductor is very large. Examples of this latter condition are found in the Mussels, Pearl-mussels, &c. On the other hand, in *Ostrea*, *Pecten*, and certain other Bivalves—hence called *Monomyaria* — the anterior adductor is absent, and the posterior adductor alone remains. The adductors leave distinct "muscular impressions" in the interior of the shell (fig. 556), so that it is easy to determine, by a simple inspection of the dead shell, whether a given Bivalve has been "dimyary" or "monomyary."

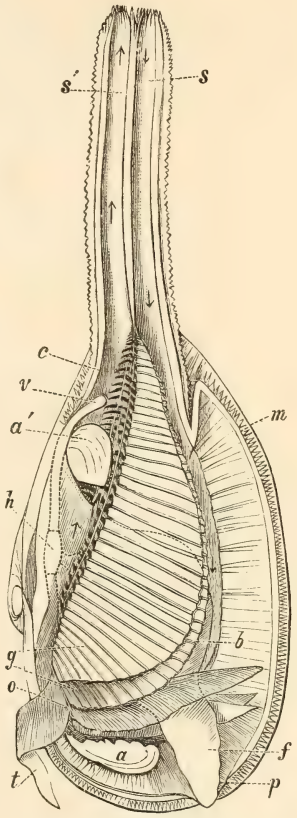


Fig. 555.—Anatomy of *Mya arenaria*. (After Woodward.) The left valve of the shell and the left mantle-lobe are removed, and half of the siphons has been cut away. *a*, Anterior adductor; *a'*, Posterior adductor; *b*, Visceral mass; *c*, Chamber of the mantle-cavity into which the anus (*v*) opens; *f*, Foot; *g*, Branchiæ; *h*, Heart; *m*, Cut ventral edge of the mantle; *o*, Mouth; *s*, Inhalant siphon; *s'*, Exhalant siphon; *t*, Labial palpi. The arrows indicate the direction of the water-currents.

Besides the scars left by the adductor muscles, or muscle, there are other impressions in the interior of the valves which are produced by the attachment of muscles. Thus, the "foot" is very commonly provided with "pedal muscles," which leave small scars in the inside of the shell. When they are well developed, the "pedal impressions" are twofold, consisting of an impression formed by the "protractor" muscle which exserts the foot, and of another, posteriorly-placed scar formed by the "retractor" muscle which withdraws the foot (fig. 556, A, *pp* and *rp*), a second retractor being sometimes inserted behind the anterior adductor.

Again, the muscular margin of the mantle is attached to the

interior of each valve along a line running at a little distance within, and parallel with, the ventral margin of the shell. In this way is formed a more or less well-marked impression in the interior of each valve, which is termed the "pallial line" (fig. 556, *m*). The form assumed by the "pallial line" differs in different Bivalves according as respiratory "siphons" are present or absent. In all those Bivalves, namely, in which the mantle-lobes are free, and in which

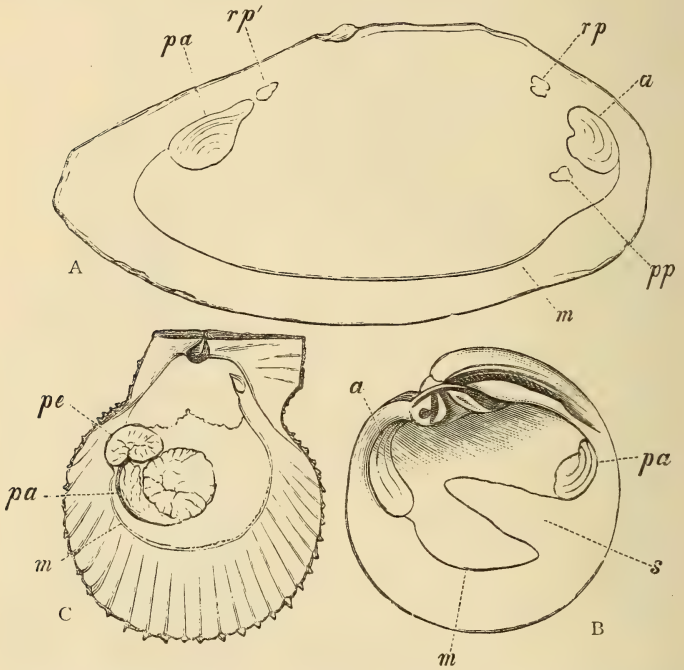


Fig. 556.—A, Interior of the left valve of *Anodonta cygnea*; B, Interior of the right valve of *Artemis exoleta* (after Woodward); C, Interior of the left valve of *Pecten varius* (after Woodward). *a*, Impression of the anterior adductor; *pa*, Impression of the posterior adductor; *m*, Pallial line; *s*, Sinus in the pallial line caused by the insertion of the retractor muscles of the siphons; *pp*, Scar of the protractor muscle of the foot; *rp*, Scar of the anterior retractor muscle of the foot; *rp'*, Scar of the posterior retractor muscle of the foot. In *Pecten varius* (C), though the shell is monomyary, the scar left by the posterior adductor (*pa*) is double, and there is a large scar (*pe*) formed by the muscular base of the foot.

there are consequently no siphons, the "pallial line" runs in an unbroken curve round the lower part of the valve (fig. 556, A, *m*). The pallial line is similarly unbroken in those Bivalves which possess short siphons, but which do not possess a specially developed "retractor muscle" for the withdrawal of the siphons within the shell. The name of *Integropallialia* is given to all such Bivalves as the above, in which the pallial line is "entire," or unindented, and there

are either no siphons or but short ones. On the other hand, in those Bivalves which have long respiratory siphons there exists on each side a specially developed "retractor muscle," the function of which is to withdraw the siphons within the shell. The insertion of this siphonal retractor causes an indentation in the pallial line posteriorly (fig. 556, B, *s*), the depth of this depending upon the size of the siphonal muscles. In all those Bivalves, therefore, which possess retractile siphons, the pallial line is deflected posteriorly into a larger or smaller "pallial sinus" or "siphonal impression;" and those Bivalves in which this sinus exists are grouped together under the name of *Sinupallialia*.

There is no distinctly differentiated head in any of the Lamellibranchs (hence the name of "Acephalous Molluscs" commonly given to the class), and the mouth is simply placed at the anterior end of the body. It is furnished with ciliated, leaf-like, membranous processes, or "labial palpi" (fig. 555, *t*), which are two or four in number, and serve to conduct the in-going water-currents to the mouth. The mouth is not furnished with any arrangement of teeth, and the animal lives upon the microscopic particles of nutrient matter brought to the mouth by the in-going currents of water, which are kept in movement by the action of the cilia covering the gills. These organs (fig. 555, *g*) are leaf-like, and are attached by their bases to the sides of the body, their free ends depending into the mantle-cavity. Most Bivalves have two of these lamellar branchiæ on each side of the body, but the external pair may be wanting.

As has been already mentioned, the arrangements for the admission of water to the gills, and its expulsion again from the mantle-cavity, are essentially the same in all Bivalves. In almost all cases the in-going current of water enters the pallial chamber posteriorly and ventrally, while the out-going current escapes posteriorly and dorsally. In those Bivalves which have free mantle-lobes ("Asiphonate Bivalves"), the apertures for the water-currents are simply produced by the apposition of the hinder edges of the mantle-lobes to each other. On the other hand, in those Bivalves which have the mantle-lobes united ("Siphonate Bivalves," fig. 555), the margins of the "inhalant" and "exhalant" apertures are drawn out or extended into longer or shorter muscular tubes or "siphons." The siphons may be separate, or they may be united to one another along one side, and they can usually be partially or entirely retracted within the shell by means of special muscles, called the "retractor muscles of the siphons." These siphons are more specially characteristic of those Lamellibranchs which spend their existence buried in the sand, protruding their respiratory tubes in order to obtain water, and with it such nutrient particles as the water may contain. As has been

previously seen, the presence or absence of retractile siphons can be readily determined merely by inspection of the dead shell.

The *Lamellibranchiata* are wholly aquatic, living in either salt or fresh water, and their habits are very various. Some, such as the Oyster (*Ostrea*), and the Scallop (*Pecten*), habitually lie on one side, the lower valve being the deepest, and the foot being wanting, or rudimentary. The former is fixed by the substance of the valve, but the latter swims by rapidly opening and closing the shell. Others, such as the Mussel (*Mytilus*) and the *Pinna*, are attached to some foreign object by a "byssus." Others are fixed to some solid body by the substance of one of the valves. Many, such as the *Myas*, spend their existence sunk in the sand of the sea-shore or in the mud of estuaries. Others, as the *Pholades* and *Lithodomi*, bore holes in rock or wood, in which they live. Finally, many are permanently free and locomotive.

The *Lamellibranchiata* have often been divided into two primary sections, according as "siphons" are or are not developed. In one of these sections—*Asiphonida*—the mantle-lobes are free, and there are no respiratory siphons, so that the pallial line is simple and is not indented. In the other great section—*Siphonida*—the mantle-lobes are more or less united, and respiratory siphons are present. In certain groups of the Siphonate Bivalves the siphons are short, without specially developed retractor-muscles, and the pallial line is therefore simple, the name of *Integropallialia* being given to such forms. On the other hand, in many types of the Siphonate Bivalves —hence termed *Sinupallialia*—there are long siphons, the greatly developed retractor-muscles of which are attached to an indentation or bay in the pallial line. This classification is doubtfully natural, and is largely inapplicable to fossil forms; for which reasons the arrangement adopted by Dr Paul Fischer in his 'Manuel de Conchyliologie' has, in the main, been here followed in preference. Owing, however, to the great importance in the study of the fossil Bivalves of the various internal markings of the shell, it may be of use here to indicate generally the principal groups of Lamellibranchs which agree with one another in the general nature of the impressions left by the pallial line and adductors; a guide being thus given to the families amongst which the affinities of a given fossil shell must be sought. From this point of view, the Bivalves fall into the four following sections, the families of which, though often allied, have no necessary zoological relationship with one another :—

(1.) The following families of *Lamellibranchiata* are "monomyary," and have an "entire" pallial line, no siphons being developed—viz., the *Ostreidæ*, *Anomiidæ*, *Spondylidæ*, *Limidæ*, and *Pectinidæ*. This group of families corresponds with the *Monomyaria* of some writers.

(2.) The following families are "heteromyary," and have no siphons, the

pallial line being "entire"—viz., the *Aviculidæ* and *Mytilidæ* (= the *Heteromyaria* of Bronn).

(3.) The following families are "homomyary," and have an "entire" pallial line, the animal being in some cases devoid of siphons, while in other cases short, non-retractile siphons are present—viz., the *Arcidæ*, *Nuculidæ*, *Modiolopsidæ*, *Trigoniidæ*, *Unionidæ*, *Cardinidæ*, *Carditidæ*, *Grammysiidæ*, *Astartidæ*, *Crassatellidæ*, *Erycinidæ*, *Galeommidæ*, *Tridacnidæ*, *Cardiidæ*, *Lunulicardiidæ*, *Chamidæ*, *Rudistæ*, *Megalodontidæ*, *Cyprinidæ*, *Ungulinidæ*, *Unicardiidæ*, and *Tancrediidæ*.

(4.) The following families are "homomyary," and are provided with retractile siphons, the pallial line thus becoming "sinuated"—viz., the *Veneridæ*, *Donacidæ*, *Psammobiidæ*, *Solenidæ*, *Mactridæ*, *Myidæ*, *Glycimeridæ*, *Gastrochænidæ*, *Pholadidæ*, *Teredinidæ*, *Lucinidæ*, *Tellinidæ*, *Scrobiculariidæ*, *Solemyidæ*, *Arcomyidæ*, *Anatinidæ*, *Præcardiidæ* (?), *Pholadomyidæ*, and *Clavagellidæ*.

As regards their general *distribution in time*, the Lamellibranchs are a very ancient group, the earliest representatives of the class (*Glyptarca*, &c.) being found in the Upper Cambrian rocks. Upon the whole, the Asiphonate Bivalves are more characteristically Palæozoic, while those in which the mantle-lobes are united and there are respiratory siphons, are principally found in the Secondary and Tertiary rocks. One of the principal Palæozoic groups is that of the *Aviculidæ*, while the *Mytilidæ* are also largely represented. Monomyary types appear in the later portion of the Palæozoic period, numerous forms (*Aviculopecten*, &c.) allied to the recent Scallops occurring in the Carboniferous rocks. With the commencement of the Secondary period, in the Trias, many old types disappear, and new ones take their places. Monomyary Bivalves are now numerous, but among the Dimyary forms the Asiphonate families still predominate. The forms with long retractile siphons (*Sinupallialia*) begin with a few types in the Trias, and gradually become more numerous as we pass upwards. The *Veneridæ*, which are perhaps the most highly organised of the groups of the Lamellibranchs, appear for the first time in the Jurassic rocks, and increasing in the Tertiaries, have culminated in the Recent period. The singular group of the *Rudistæ* is exclusively confined to the Cretaceous period.

CHAPTER XXXVI.

LAMELLIBRANCHIATA—continued.

DIVISIONS OF LAMELLIBRANCHIATA.

VARIOUS attempts have been made to divide the *Lamellibranchiata* into sections equivalent to the "orders" of the higher animals, but, so far, little success has attended these efforts, and no arrangement which has hitherto been proposed can be regarded as thoroughly satisfactory, more especially from a palæontological point of view. In what follows, the *Lamellibranchiata* are divided into a number of sections, which it is convenient to speak of as so many "orders," though it cannot be asserted that they have a value equivalent to the divisions known by this title among Vertebrate animals. As regards these primary sections, Dr Paul Fischer has been followed, and under each section will be given the characters and geological range of the more important families included in it.

ORDER I. OSTREACEA.

In this order the mantle-lobes are completely free; a single adductor muscle (the posterior) is alone present, the animal being thus "monomyary"; there are two branchiæ on each side of the body; and the foot is wanting, or is present in a rudimentary form and secretes a "byssus." The shell is inequivalve; the hinge is edentulous; the ligament is internal; and the pallial line is "entire," and sometimes not distinct. This order includes the two families of the *Ostreidæ* and *Anomiidæ*.

FAMILY 1. OSTREIDÆ.—In this family the shell is generally inequivalve and fixed to foreign bodies by the substance of the left valve, but is in other cases free; the beaks are subcentral, or, in many cases, twisted; the ligament is internal, and is lodged in a triangular cartilage-pit; the single muscular impression is subcentral, or excentric and posterior; the pallial line is not distinct; and the

shell-structure is laminated. This family is exclusively confined to salt water, and comprises the Oysters. Numerous Secondary and Tertiary representatives of the family are known, but the few Palæozoic types which have been referred here are probably really of a different nature.

The principal genus included in the *Ostreidæ*, as here understood, is *Ostrea* itself, the essential characters of which are those of the

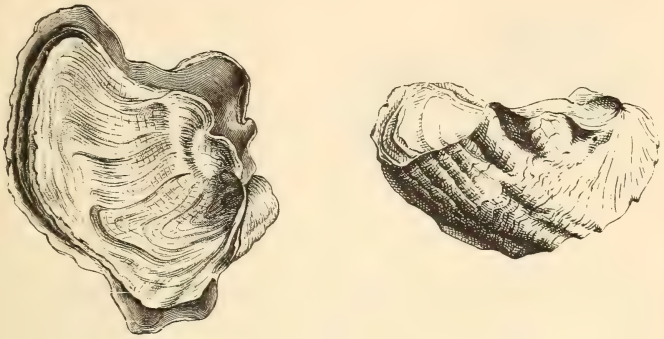


Fig. 557.—*Ostrea* (*Exogyra*) *Couloni*. Lower Greensand.

family itself. The shell described by De Koninck from the Carboniferous Limestone under the name of *Ostrea nobilissima* has generally been quoted as the oldest known type of the genus *Ostrea*, but it is referred by Fischer to the genus *Pachypteria* (*? Spondylidæ*). In the Secondary and Tertiary rocks, however, we meet with a vast

Fig. 558.—*Ostrea* (*Alectryonia*) *Marshii*. Oxford Clay (Middle Oolites).

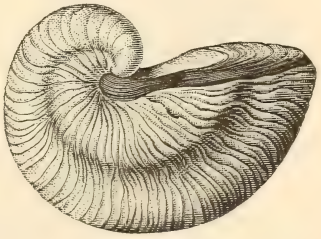


Fig. 559.—*Gryphæa incurva*. Lias.

number of fossil Oysters, which have commonly been distributed among several more or less well-marked sections of the genus, of which the following are the most important. In the typical forms of the genus (*Ostrea* proper) the valves are pretty nearly of the same length, the lip of the right valve is not serrated, and the external

surface is marked with concentrically-disposed foliaceous ridges or with roughly radial ribs. The umbo is not incurved, and below it is a transversely striated ligamental pit. The Edible Oyster (*O. edulis*) is a familiar example of this section of the genus, and essentially similar forms are known to have existed in the Jurassic rocks. In the sub-genus *Alectryonia* (fig. 558) both the valves are strongly ribbed or folded, the edges of the valves being thus indented in a

Fig. 560.—*Exogyra aquila.* Lower Greensand.

zigzag manner; while the adductor impression is placed far back. Forms of this type began to exist as early as the Trias, and the recent *O. crista-galli* is a familiar example of a now living form of the group.

In the sub-genus *Gryphæa* (fig. 559), the two valves are of unequal length, the left valve fixed in early life, but often becoming free in the adult condition, while its beak is prolonged and incurved, being bent either forwards or backwards. The right valve, on the other hand, is small in size, and is flat or concave in shape, looking like a kind of operculum to the left valve. The species of *Gryphæa*

Fig. 561.—*Exogyra virgula.* Upper Oolites.

are pre-eminently Jurassic and Cretaceous, but a few Tertiary and Recent forms of the group are known.

In the sub-genus *Exogyra*, again, the shell is very inequivalve (figs. 557, 560, and 561), and is fixed by the substance of the thick and concave left valve, the right valve being flat and resembling an "operculum" in form. The beaks of both valves are rolled up, being "reversed"—that is to say, turned towards the posterior side

of the shell—and the ligamental area is oblique and narrow. The species of *Exogyra* are abundant in the Jurassic and Cretaceous deposits.

The name of *Pernostrea* has been proposed by Munier-Chalmas for certain Jurassic Oysters which differ from *Ostrea* proper chiefly in having the ligament contained in from four to eight transverse grooves or pits (as in *Perna*).

Family 2. Anomiidæ.—In this family the shell is inequivalve, and is fixed to foreign objects, either in early life or permanently, by a byssus, which traverses a notch or foramen in the right valve, and is ordinarily calcified at its termination. The muscles of the byssus leave one or more impressions on the interior of the left valve. There is an internal ligament; the hinge is edentulous; the pallial line is simple; and the shell exhibits a laminated structure. The range of the family is from the Devonian to the present day, and the chief genera are *Anomia* and *Placuna*.

In the genus *Anomia* (fig. 562) the shell is suborbicular and ostreiform, the left or upper valve being convex, while the right or under valve is flat or concave. In the margin of the right valve, near

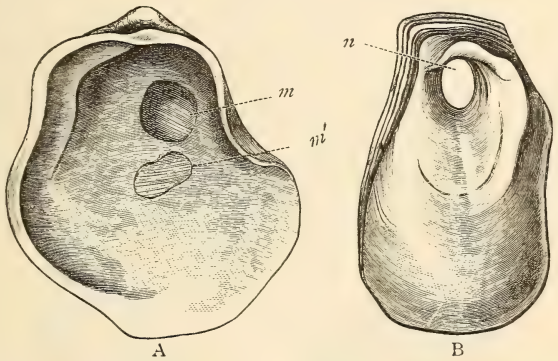


Fig. 562.—*Anomia Casanovei*, from the Eocene Tertiary, enlarged. A, Interior of the left valve; B, Interior of the right valve: *n*, Foramen for the passage of the byssus; *m*, Impressions left by the muscles of the byssus; *m'*, Adductor impression. (After Hoernes.)

the hinge, is a deep notch or sinus, which in process of growth may be converted into a complete foramen, and which serves to transmit the byssus, by means of which the shell is attached to foreign bodies. The end of the byssus is calcified, and it forms a solid plug which fills up the notch or foramen in the valve. The interior of the right valve shows only the impression of the single adductor, but the interior of the left valve exhibits in addition one to three scars produced by the muscles of the byssus. All the living forms of *Anomia* are marine, and the genus is represented in past time by numerous

Tertiary species, and, more rarely, by Cretaceous and Jurassic types. The *Limanomia* of the Devonian rocks is, however, very closely related to *Anomia* proper, from which it differs in the pointed shape and radial striation of the valves, and in the fact that the byssal foramen is trigonal in form.

The extinct genus *Placunopsis*, ranging from the Carboniferous Limestone to the Jurassic, resembles *Anomia* in many respects, but the right valve is not perforated; the ligament is lodged in a transverse, submarginal groove; and the adductor impression is large and subcentral. The genus *Placuna* comprises flattened and cake-like, orbicular shells, which are unattached to foreign bodies. The elastic ligament is supported by two diverging ridges in the right valve, with corresponding grooves in the left valve. The typical forms of the genus are recent, but types of no more than sub-generic value occur in the Tertiary rocks. The Jurassic genus *Hypotrema* is intermediate between *Anomia* and *Placuna*, since it possesses a byssal foramen which is completely closed in the adult.

Order II. Pectinacea.

In this order, the mantle-lobes are completely free; there is a single adductor only; there are no siphons; there are two branchiæ on each side of the body; and the foot is rudimentary and often byssiferous. The shell-structure is tubulated or lamellated, but without a proper prismatic layer. The shell is inequivalve or sub-equivalve; the ligament is lodged in a pit between the beaks; the hinge is generally toothed; and the pallial line is entire. This order contains the three principal families of the *Spondylidæ*, *Limidæ*, and *Pectinidæ*, all the recent forms of which are marine.

Family 1. Spondylidæ.—In this family the shell is inequivalve,

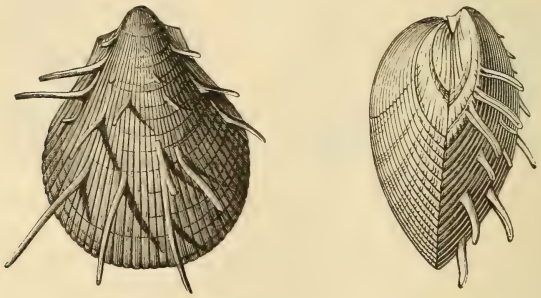


Fig. 563.—*Spondylus spinosus.* Chalk.

and is attached to foreign bodies by the beak of the right valve, which is larger than the left. The hinge of each valve has two teeth, between which is the cartilage-pit. The adductor impression

is subcentral. The two principal genera of this family are *Spondylus* and *Plicatula*.

The genus *Spondylus*, comprising the "Thorny Oysters," has an equivalve shell, the right valve being the deepest, and serving for the attachment of the shell to foreign bodies (fig. 563). The beaks are separated and are eared, and the shell is covered with spines, foliaceous expansions, or ribs radiating from the beak. The lower valve has a triangular hinge-area, and there are two teeth in each valve. The *Spondyli* seem to have commenced in the Jurassic period (? Trias), are abundant in the Cretaceous, and have continued through the Tertiary period to the present day.

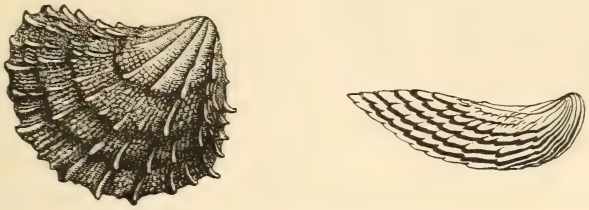


Fig. 564.—*Plicatula placunea*. Lower Greensand.

The genus *Plicatula* (fig. 564) approaches *Spondylus* nearly in having an inequivalve shell, which is attached by the right valve, and by having two hinge-teeth in each valve. The shell, however, is rarely eared, the hinge-area is obscure, and the valves are not spiny, though they may be plaited. The *Plicatulæ* extend from the Trias to the present day, and they abound to such an extent in parts of the Lower Greensand (Cretaceous), as to have given rise to the name of "Argile à Plicatules" applied to the beds in question. Lastly, the genus *Terquemia*, of the Triassic and Liassic rocks, resembles *Spondylus* in many respects, but is at once distinguished by the fact that the hinge is edentulous. In this respect the genus resembles the Oysters, from which it is separated by the fact that the shell is attached by the *right* valve, and not by the left. Fischer also includes in this family, with doubt, the Carboniferous genus *Pachypteria*.

Family 2. Limidæ.—The shell in this family is auriculate, and equivalve or nearly so, and it may be free or may be attached by a byssus, which passes out by a sinuosity in the right valve or by a notch below the anterior ears. The beaks are pointed and straight, and a portion of the hinge-area and ligament is left externally visible; while hinge-teeth may be wanting or present. The earliest types of the family appear in the Carboniferous rocks; there are numerous Secondary and Tertiary forms; and the present seas contain a limited number of existing species.

In the genus *Lima* or *Radula* the shell is equivalve and free, and the beaks are separated from one another and eared (fig. 565). The surface is generally adorned with radiating ribs or striæ, and there is a median cartilage-pit, and a triangular hinge-area. The genus (including *Plagiostoma*) appears to occur in the Carboniferous, is abundantly represented in the Triassic, Jurassic, Cretaceous, and Tertiary rocks, and exists in diminished numbers at the present day. *Limea*, ranging from the Trias to the Recent period, differs from *Lima* principally in having the hinge-line closely toothed.

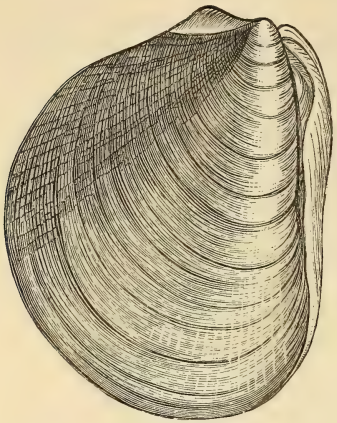


Fig. 565.—*Lima* (*Plagiostoma*) *gigantea*. Lias.

Family 3. Pectinidæ.—In this family the foot is tongue-shaped and byssiferous; the margins of the mantle-lobes carry ocelli; and the adductor impression is a little excentric. The shell is sub-equivalve or equivalve, nearly equilateral, auriculate, free or occasionally attached by the right valve. Generally there is a notch under the ear of the right valve for the passage

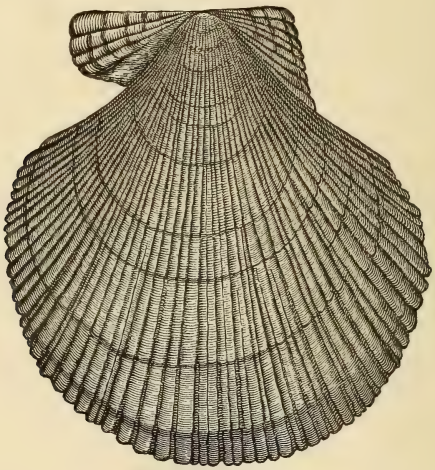


Fig. 566.—*Pecten Islandicus*, left valve. Post-Tertiary and Recent.

of the byssus; and the cartilage-pit is internal, of triangular shape, and placed between the beaks, being rarely broken up into detached pits. All the members of this family are marine, its earliest forms

appearing in the Devonian rocks, while numerous living types exist.

The genus *Hinnites* comprises a number of forms in which the shell is free when young, but becomes in adult life attached by the right valve, the shell becoming at the same time thick and irregular. The left valve is free, and the hinge-line is edentulous. Numerous fossil forms of *Hinnites* are known, the earliest appearing in the Trias, and the genus still survives.

In the genus *Pecten*, comprising the Scallops, the shell (fig. 566) rests upon the right valve, and the beaks are furnished with ears. The anterior ears are the largest and most prominent, and the shell is generally furnished with ribs radiating from the umbos. There is a single, median, triangular cartilage-pit. The right valve is the deepest, and is notched for the byssus below the anterior ear. Using the name *Pecten* in its modern and restricted signification, it is probable that all the Palæozoic shells so named are really referable to allied genera (*Aviculopecten* and *Pernopecten* more especially). The genus, however, is largely represented both in the Secondary and Tertiary deposits, and exists under numerous and varied forms at the present day.

The name of *Entolium* has been given to forms of *Pecten* in which the shell is smooth, the hinge-line is rendered angular by the outward extension of the ears, and there is no byssal notch under the anterior ear of the right valve. Numerous forms of this type occur from the Jurassic onwards; but the Palæozoic shells which have been placed here are probably referable to allied genera, such as *Pernopecten*. In the genus *Pernopecten*, of the Devonian and Carboniferous rocks, are comprised ancient types of Scallops, with small, nearly equal, ears, the central triangular cartilage-pit being flanked by a row of smaller pits on each side (thus approaching *Perna*), and the surface being nearly or quite devoid of radiating ridges. The genus *Crenipecten*, with a similar geological range to *Pernopecten*, has the hinge furnished with a row of small cartilage-pits along its entire length, no central pit being present.

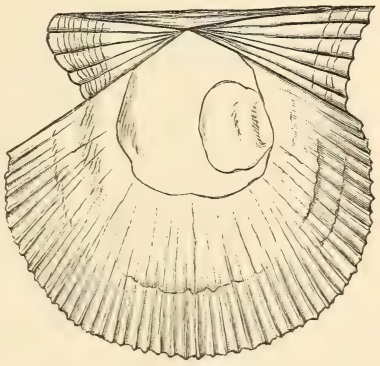


Fig. 567.—Internal cast of *Aviculopecten*. Carboniferous. (After M'Coy.)

Of the Palæozoic types of the *Pectinidæ*, the most important is the large and widely distributed genus *Aviculopecten*, which, as its name implies, affords a transitional link between the present family

and that of the *Aviculidæ*. The shell in this genus (fig. 567) has the general form and aspect of that of *Pecten* itself; but the anterior ear is flattened, and *smaller than the posterior one*. There is a byssal notch beneath the anterior ear; but there is no median cartilage-pit, and the ligament is confined to a narrow facet along the hinge-margin. The muscular impression and pallial line are as in *Pecten*. The hinge-line is usually shorter than the transverse diameter of the shell, and the surface is generally adorned with radiating ribs. The species of *Aviculopecten* are distributed between the Devonian and Permian, but they are most characteristic of the Carboniferous rocks, in which they are extremely abundant. In the absence of a median cartilage-pit, and the lodgment of the ligament in a groove along the hinge-line, the genus approaches the *Aviculidæ*, but its shell is stated by Meek to have the corrugated and laminated structure of *Pecten*, and not the prismatic structure of the former. The genus *Streblopteria* of the Carboniferous and Permian rocks comprises forms which agree with *Aviculopecten* in having the ligament in a groove along the margin of the ears; but the posterior ear is hardly marked off from the hinder margin of the shell, and an oblique posterior cardinal tooth is present.

Order III. Mytilacea

(= *Heteromyaria*, Bronn).

In this order the mantle-lobes are free, the pallial line is entire, and there are usually two adductor muscles. (In the Tertiary genus *Dreissenomya* the pallial line is sinuated; while the recent genus *Prasina* is monomyary.) The anterior adductor is small; the posterior is of large size. The foot is tongue-shaped and usually byssiferous. The shell possesses an external, often largely developed, prismatic layer, and may be inequivalve or equivalve. The ligament is generally contained in several marginal grooves or in an oblique furrow; and the hinge may or may not be provided with teeth. The two principal families contained in this order are the *Aviculidæ* and *Mytilidæ*, and the recent forms are in part marine, and in part inhabitants of fresh waters.

Family 1. Aviculidæ.—In this family the mantle-lobes are free, the foot is small and byssiferous, and the shell-structure consists of an internal nacreous layer and an external prismatic layer. The anterior adductor [1] is small, and leaves its impression at the base of

[1] The muscle which is here spoken of as the "anterior adductor" is sometimes regarded as, in some cases, being really the anterior retractor of the foot. On this view, there is no anterior adductor muscle in some of the most typical forms of the *Aviculidæ*, the animal being monomyary.

the anterior ear; the posterior adductor impression is large and subcentral. The shell is inequivalve or subequivalve, oblique, with a straight hinge-line, and furnished on one or both sides with wing-like expansions or ears. Under the anterior ear of the right valve is a notch or aperture for the transmission of the byssus. The family of the *Aviculidæ* is a very large one, and has a most extensive development in past time, beginning under various types in the Ordovician rocks, and being continued thereafter to the present day. The principal forms included in this family may be briefly considered under the following groups :—

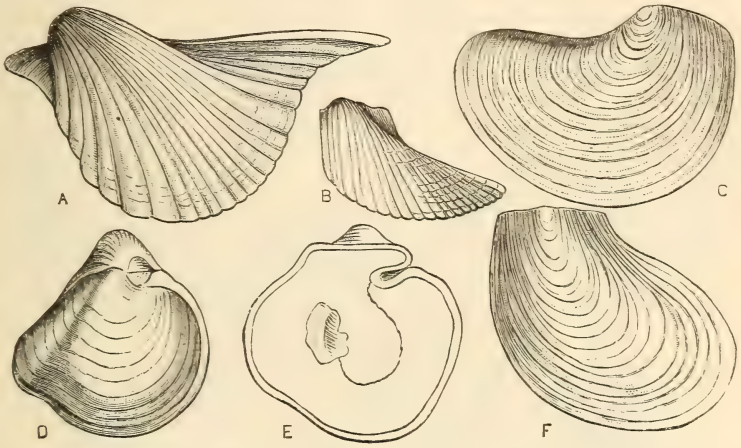


Fig. 568.—Types of *Aviculidæ*. A, *Avicula Cottaldina*—Cretaceous; B, *Avicula contorta*—Upper Trias; C, *Vulsella falcata*—Eocene; D, *Pseudomonotis speluncaria*—Permian; E, Interior of the shell of the same, showing the adductor impression and pallial line; F, *Posidonomya Becheri*—Lower Carboniferous.

Firstly, we have the great group of shells, of which *Avicula* itself (fig. 568, A and B) is the type. In this genus the shell is oblique and inequivalve, the right valve being smaller and less convex than the left. The right valve has a byssal notch under the anterior ear, and the hinge has one or two cardinal teeth, sometimes with an elongated posterior tooth. The ligament is partly external, partly contained internally in a deep groove. The species of *Avicula* range from the Ordovician period to the present day, numerous forms of this genus occurring in the Secondary and Tertiary rocks.

More or less closely allied to *Avicula* are the Palæozoic genera *Leiopteria* (Devonian and Carboniferous), *Monopteria* (Carboniferous), *Pterinites* (Devonian and Carboniferous), *Limoptera* (Devonian), and *Eopteria* (Ordovician). Also related to *Avicula* is the genus *Pseudomonotis* (*Eumicrotis*, Meek), in which the shell is but slightly oblique, and is inequivalve,

the left valve convex, with a prominent beak. The hinge is nearly or quite toothless, and the anterior ear is small or undeveloped, while a deep byssal notch in front is present (fig. 568, D and E). The earliest forms of *Pseudomonotis* are found in the Devonian rocks, but the genus attains its maximum in the Triassic and Jurassic rocks. A well-known species from the Permian rocks of Europe is *P. speluncaria* (fig. 568, D). In the singular Triassic genus *Cassianella* (fig. 570, D and E) the shell is thick and very inequivalve, the right valve being flat or concave, while the left is strongly convex. The hinge-line is straight, with few teeth, the ligament being lodged in a triangular groove behind the beaks; a byssal notch is absent; and the shell is eared.

Another, but limited, group is that represented by *Vulsella* and *Malleus*, together with some Secondary and Tertiary forms of small importance, characterised by the common feature that the ligament is lodged in a single pit extending from the beak internally. In *Vulsella* (fig. 568, C) the shell is nearly equivalve and earless, the hinge being toothless, and a byssal notch being absent. The genus dates from the Eocene Tertiary, and still survives. On the other

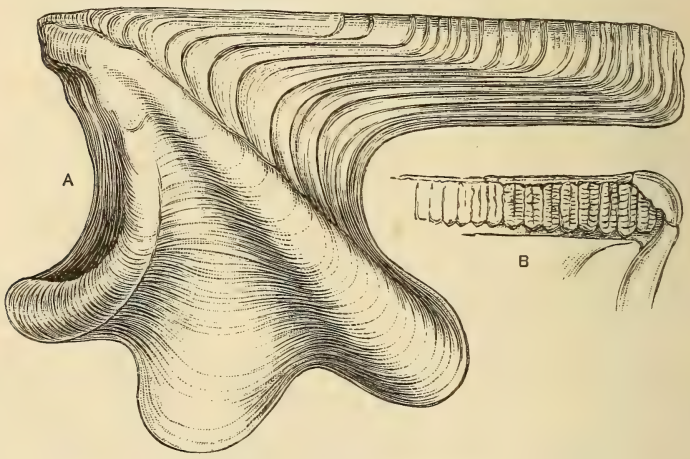


Fig. 569.—*Perna Mulleti* (A), and a portion of its hinge-line (B). Lower Greensand.

hand, the "Hammer-oysters" (*Malleus*) are not known in the fossil state, and are distinguished by their very long ears and central beaks.

A third, much more important, group of the *Aviculidæ* is that represented by *Perna* and its allies, all of which have a straight hinge-line, crossed by numerous transverse furrows for the lodgment of the ligament. In *Perna* (or *Melina*) itself (fig. 569) the shell varies in form, but there is generally a long posterior ear; there are numerous close-set cartilage-pits, and the right valve has a byssal

notch. The genus begins in the Trias, is well represented in the later Secondary and Tertiary deposits, and still survives under a few forms. A large and well-known species is the *Perna Mulleti* of the Neocomian rocks. Allied to the preceding is the genus *Gervillia* (fig. 570, A), in which the shell is elongated and very oblique, with a broad and wing-like posterior ear. The hinge-line is furnished with numerous cartilage-pits (fig. 570, B), and the anterior ear is comparatively small, while the beaks are nearly or quite terminal in position. The species of *Gervillia* abound in the Triassic, Jurassic, and Cretaceous rocks, and a single species of the

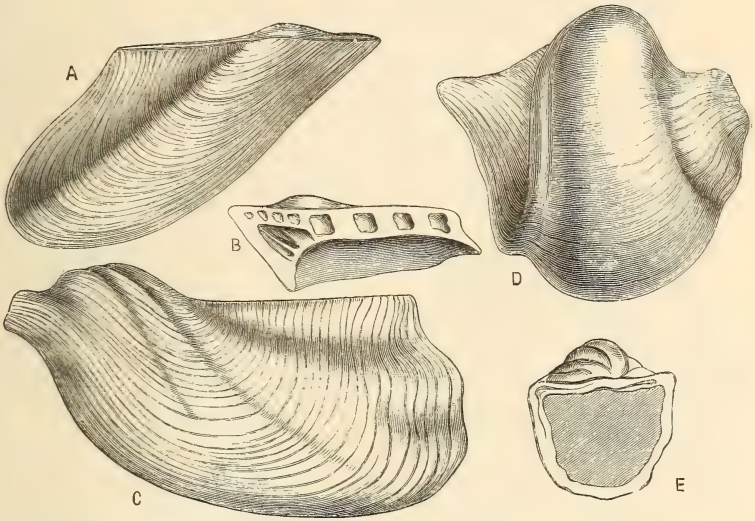


Fig. 570.—Types of *Aviculidæ*. A, *Gervillia Hartmanni*—Lias; B, Part of hinge of the same, enlarged; C, *Hoërnesia Joannis-Austriæ*, slightly enlarged—Trias; D and E, *Cassianella gryphæata*, of different ages—Trias. (After Münster and Laube.)

genus is found in the Eocene rocks. In the Trias are found various forms of the closely allied *Hoërnesia* (fig. 570, C), in which the left valve is greatly inflated, with a strongly incurved beak, while the hinge-line is crenulated, and a single strong tooth exists in both valves. *Bakewellia*, of the Permian, resembles *Gervillia* in general form, but the hinge is provided with anterior and posterior teeth, and the cartilage-pits are few in number. The Devonian genus *Actinodesma* is probably a still older relative of *Gervillia*.

Nearly related to both *Gervillia* and *Perna* is the important and widely-distributed genus *Inoceramus* (figs. 571, 572), which is entirely confined to the Secondary period, and is mainly characteristic of the Cretaceous series. The shells of this genus are inequivalve, with

radiating ribs or concentric furrows, and with prominent beaks. The shell is earless, and the hinge-line is long and straight, with numerous cartilage-pits. Some of the *Inocerami* attain a length of

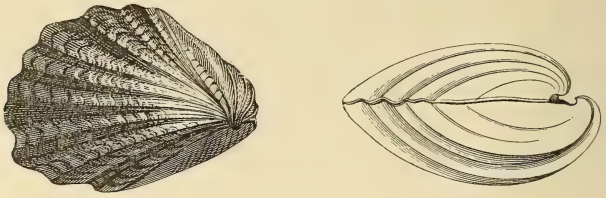


Fig. 571.—*Inoceramus sulcatus.* Gault (Cretaceous).

two or three feet, and fragments of them are often found perforated by boring sponges. The shell in the *Inocerami* consists of a thin internal nacreous layer, with a generally very thick outer prismatic

Fig. 572.—*Inoceramus problematicus.* Chalk.

stratum, but either the internal or the external layer may be destroyed in the process of fossilisation.

The Jurassic and Cretaceous genus *Aucella* (fig. 573) is related to the preceding, but may be considered as the type of a separate group of the *Aviculidæ*. In this genus, the shell (fig. 573) is very inequivalve, the left valve being convex and the right valve flat, and the beaks of both valves being inflated and incurved. The ears are imperfectly developed; the surface is concentrically striated; the ligament is external and linear; and the hinge is hardly or not at all toothed. The Carboniferous genera, *Rutotia*, *Posidoniella*, and *Aphanaia*, and the Triassic genus *Rhynchopterus*, are placed by Fischer in the same group with *Aucella*.

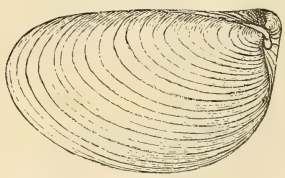


Fig. 573. — *Aucella mosquensis*, Upper Jurassic, Russia. (After Zittel.)

The genus *Monotis* is the type of another group of the *Aviculidæ*, in which the shell is equivalve, compressed, with small beaks, the ears more or less confluent with the shell, the hinge without teeth, and the ligament linear. *Monotis* itself is confined to the Trias, occurring in rocks of this age in both the Old World and the New. Very closely related to the preceding are the Triassic genera *Dao-*

nella (fig. 574) and *Halobia*, in which are comprised flat, equivalve, radiately-striated shells, more or less markedly inequilateral in shape, with a straight hinge-line, without a ligamental pit or teeth, and with no ears. Also belonging to this group is the remarkable genus *Posidonomya* (=*Posidonia*), in which the shell (fig. 568, F) is thin, concentrically striated, with a straight hinge-line, destitute of hinge-teeth, and without developed ears. The species of *Posidonomya* range from the Silurian to the Jurassic rocks, and have a general resemblance in shape to specimens of *Estheria*. The species of this genus commonly occur gregariously, and particular species are commonly characteristic of particular horizons.

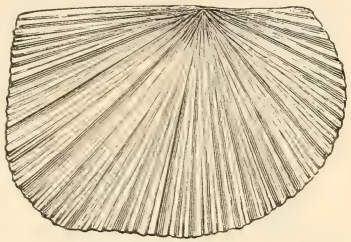


Fig. 574.—*Daonella* (*Halobia*) *Lommelli*. Trias.

The important Palæozoic genus *Pterinea* is the type of another group of the *Aviculidæ*, in which the shell (figs. 575, 576) is equi-

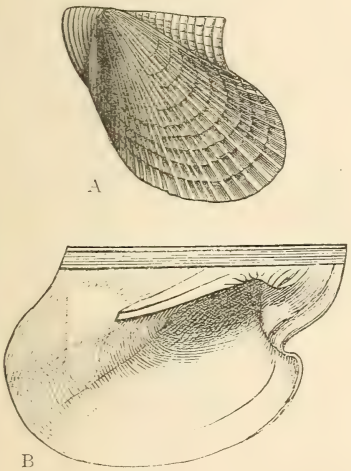


Fig. 575.—A, *Pterinea subfalcata*, Silurian. (After M'Coy.) B, Interior of the left valve of *Pterinea lævis*, Devonian. (After Zittel.)

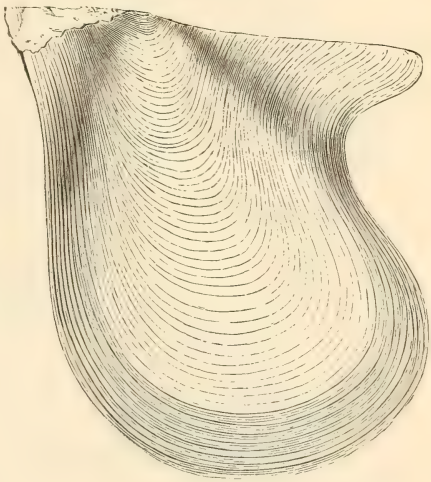


Fig. 576.—*Pterinea* (*Avicula*) *demissa*. Ordovician rocks (Hudson River group) of North America.

valve, inequilateral, and winged, with a byssal notch below the anterior ear. The hinge has two or more cardinal teeth, with oblique lateral teeth, and there is a large, longitudinally-striated ligamental area for the reception of the internal ligament. The

small impression of the anterior adductor is placed below the anterior ear, and the surface is radiately striated. The species of *Pterinea* have a wide distribution in the Ordovician, Silurian, Devonian, and Carboniferous rocks. The Devonian genus *Glyptodesma* is allied to *Pterinea*, but the ligament is external, and the hinge has two strong lateral teeth, together with numerous irregular transverse plications along its margin.

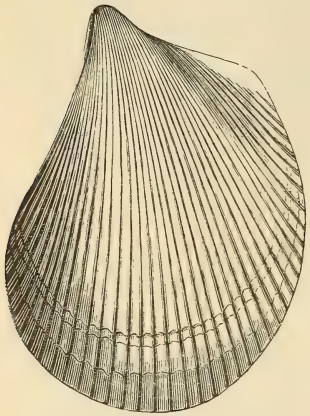


Fig. 577.—*Ambonychia radiata.* Ordovician.

The genus *Ambonychia* (fig. 577) is the type of another group of the *Aviculidæ*, and is widely distributed in the Palæozoic rocks, ranging from the Ordovician to the Carboniferous. In this genus the shell (fig. 577) is equivalve and very inequilateral, the beaks being pointed, and placed at the anterior end of the long straight hinge-line. The ligament is internal, and is lodged in longitudinal grooves running parallel with the cardinal margin. There is no anterior ear, but a wide byssal aperture is present, while the posterior ear is broad and aliform. The Devonian genera *Mytilarca* and *Gosseletia* may be placed in the neighbourhood of *Ambonychia*.

A transition between the *Aviculidæ* and the *Mytilidæ* is effected

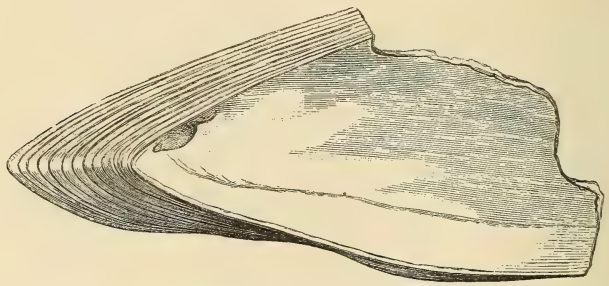


Fig. 578.—*Myalina crassa*, interior of a broken right valve, showing the hinge. Carboniferous Limestone. (Original.)

by the remarkable genus *Myalina* (fig. 578), in which the shell is inequivalve, and mussel-shaped, with terminal beaks, and a flat and thickened cardinal area marked with longitudinal cartilage-grooves, and sometimes with the umbones septate. The genus *Myalina* is

stated to range from the Silurian to the Permian, but it is principally characteristic of the Carboniferous and Permian rocks. Though the shell of *Myalina* resembles that of the *Mytilidæ* in form, the shell-structure agrees with that of the *Aviculidæ* in the presence of a well-developed external prismatic layer.

We pass naturally from the *Aviculidæ* to the *Mytilidæ* through the genus *Pinna* and its allies, which have often been regarded as constituting a special family (*Pinnidæ*). In *Pinna*, the type-genus

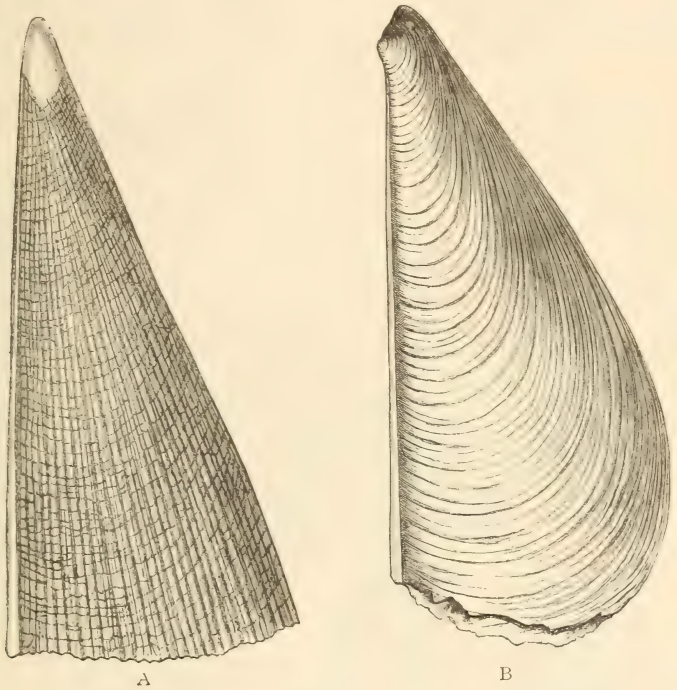


Fig. 579.—A, *Pinna flabelliformis*, the hinder part of the shell being broken away, reduced in size; B, *Aviculopinna membranacea*. From the Carboniferous Limestone of Belgium. (After De Koninck.)

of this group, the shell (fig. 579) is equivalve and wedge-shaped; the beaks are placed quite at the anterior end of the shell, and the posterior end is truncated and gaping. The hinge is toothless, and there is an elongated ligamental groove. The shell consists almost entirely of the external prismatic layer, the inner nacreous layer being of extreme tenuity. The earliest types of *Pinna* appear in the Devonian rocks, and some of these have been separated by Hall to form the genus *Palæopinna*, on the ground of the convexity

of their valves and the fine striation of the surface. In the Carboniferous rocks the genus is represented by large forms, and numerous later types are known, the existing species having a wide range in space.

In the Jurassic and Cretaceous genus *Trichites* the shell is of large size and great thickness, with a marked fibrous structure, the valves being of unequal size, with twisted beaks and undulated margins. The hinge-line is linear and edentulous, and the impression of the posterior adductor is very long and narrow. Lastly, in the Carboniferous and Permian genus *Aviculopinna* (fig. 579, B), the beaks are placed a little way behind the anterior extremity of the shell, and the surface is nearly smooth, and is marked with concentric striæ.

Family 2. Mytilidæ.—In this family the foot is cylindrical, grooved, and byssiferous, and there are two adductor impressions, that of the anterior adductor being small and terminal in position, while that of the posterior adductor is of large size. The shell is mostly equivalve, wedge-shaped or oval, with anteriorly-placed beaks, not alate, and without a byssal notch; the byssus passing between the slightly gaping ventral margins of the valves. The cardinal margin is oblique; the hinge is edentulous; and the ligament is long, linear, and marginal. The pallial line (except in *Dreissenomya*) is entire. The shell is composed of an inner nacreous layer and an outer cellulo-prismatic stratum, with a horny epidermis. The *Mytilidæ* are partly marine and partly inhabitants of brackish or fresh water, and the earliest types of the family appear to be found in the Devonian rocks.

In the genus *Mytilus* are the true "Mussels," in which the shell is very inequilateral and wedge-shaped, and the beaks are terminal in position. Numerous fossil forms are known, commencing in the Trias, and the genus is largely represented at the present day. The Palæozoic shells which have been placed under *Mytilus* probably belong really to other genera. The genus *Modiola*, comprising the "Horse-mussels," is hardly separable, so far as the shell is concerned, from *Mytilus* proper, the principal differences being that the shell is rather oblong than cuneiform, and the beaks are rounded, and are placed a little behind the anterior extremity (fig. 580). The genus *Modiola* appears to be

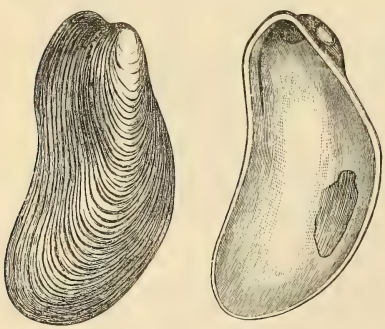


Fig. 580.—Exterior and interior of the left valve of *Modiola subcarinata*, from the Eocene Tertiary of the Paris Basin.

represented in formations as ancient as the Devonian and Carboniferous, but most of the fossil species are Secondary and Tertiary, and there are also numerous living forms. The Recent and Tertiary genus *Septifer*, again, differs from *Mytilus* in having a calcareous shelf within the beak for the attachment of the anterior adductor muscle. The "Date-shells" (*Lithodomus*) are nearly related to *Modiola*, and are distinguished by their long, cylindrical, anteriorly-inflated shell, and by their habit of forming perforations in rocks, in which they live. They appear to date from the Carboniferous rocks, and are known to palæontologists by both their shells and their burrows. *Crenella*, of the Cretaceous, Tertiary, and Recent deposits, is another ally of *Modiola*.

The genus *Dreissena* (including *Congeria*) comprises Mussel-shaped Bivalves, with terminal beaks (fig. 581), and a small byssal notch in the right valve, but differing from *Mytilus* in having keeled valves, and in the fact that the internal lining of the shell is not nacreous. The hinge is toothed, and the anterior adductor is attached (as in *Septifer*) to a calcareous shelf within the beak. The living species of *Dreissena* are inhabitants of fresh or brackish

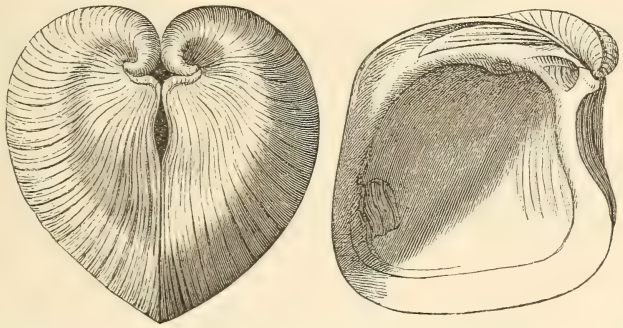


Fig. 581.—*Dreissena* (*Congeria*) *conglobata*, from the Upper Miocene of the Vienna basin. (After Zittel.)

waters, and have a very wide distribution. Fossil forms of the genus are found, often in extraordinary profusion, in the Miocene and Pliocene deposits of Central and Eastern Europe, certain of the Tertiary beds of Austria and Hungary being, for this reason, spoken of as the "Congerien-schichten." The Miocene genus *Dreissenomya* is related in most respects to *Dreissena*, but exhibits the remarkable feature that the pallial line is sinuated.

It is, lastly, probable that the thin-shelled Carboniferous Bivalves which constitute the genus *Anthracoptera* are brackish-water forms, and are allied to *Dreissena*. In general form *Anthracoptera* re-

sembles *Myalina*, but it is destitute of the thick striated hinge-plate of the latter, and the ligament is external.

Order IV. Arcacea.

In this order the mantle-lobes are completely separate, or may form two respiratory siphons; the foot is byssiferous or grooved; and there are two adductors. The shell is ordinarily equivalve, and the hinge is furnished in both valves with a series of equal and similar teeth. This division of Bivalves includes the two families of the *Arcidæ* and *Nuculidæ*, both of which have representatives in rocks as ancient as the Ordovician, at any rate.

Family 1. Arcidæ.—In this family the muscular impressions are nearly equal, the foot is large, bent, and deeply grooved, and the mantle-lobes are separate. The shell is equivalve, and the hinge is long and carries numerous comb-like teeth. The ligament is usually external, attached to a striated area below the beak, but it may be internal, and contained within a single groove. The family of the *Arcidæ* appears to be represented in the Upper Cambrian deposits (*Glyptarca*) and is largely developed in existing seas.

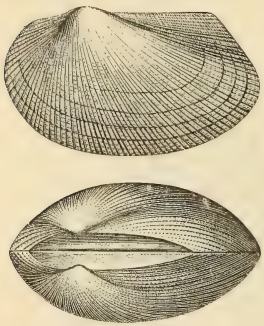


Fig. 582.—*Arca antiqua*. Permian.

In the genus *Arca* (fig. 582) the shell is transversely elongated and inequilateral, the surface being generally ornamented with radial ribs or striæ. The hinge-line is straight, and is furnished with numerous transverse equal teeth. The beaks are remote from one another, and are separated by an oval or lozenge-shaped, striated ligamental area. Taken as a whole, the genus *Arca* ranges from the Upper Cambrian to the present day, the oldest types (*Glyptarca*) appearing in the Lower Tremadoc beds.

The genus *Arca* has been broken up into numerous sub-genera, of which the two most important are *Carbonarca* and *Isoarca*. The former of these comprises some types from the Carboniferous Limestone, in which the beaks are tumid and incurved, and the hinge has two strong oblique teeth in front, and numerous transverse teeth behind. The forms included under the head of *Isoarca* belong to the Jurassic and Cretaceous rocks, and have an elongated, very inequilateral shell, with the beaks near the anterior end. The beaks are inflated and incurved, and the hinge-line is slightly curved, and has a row of transverse teeth on each side.

Closely allied to *Arca* is the genus *Cucullæa*, in which the shell is trapezoidal and ventricose; the hinge-line is straight; and the hinge-

teeth are few and oblique, and at each end of the hinge become parallel with the cardinal margin. The genus *Cucullæa*, in the wide sense, ranges from the Carboniferous period to the present day, but it is a matter of great difficulty to separate the fossil forms of this genus from those belonging to *Arca*.

The genus *Cucullæa* has been divided into sub-genera, of which the two most important are *Macrodon* and *Parallelodon*. In the former of these (fig. 583, E) the shell is greatly elongated, with a long hinge-line, the portion of which in front of the beaks carries a number of short

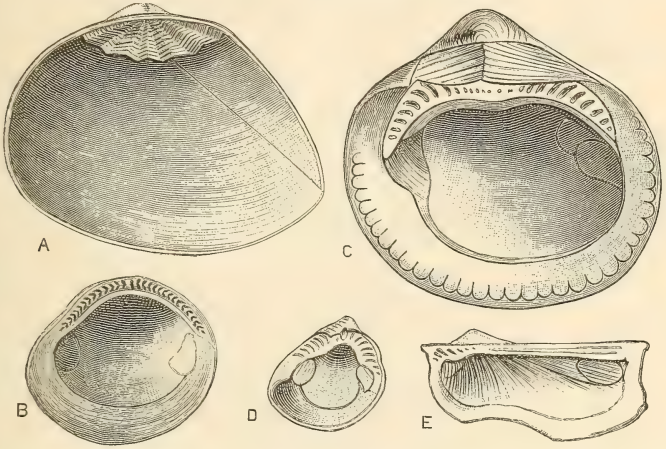


Fig. 583.—Types of *Arcidæ* and *Nuculidæ*. A, Interior of *Lyrodesma Cincinnatiensis*, showing the hinge, enlarged three times—Ordovician (after Hall); B, Interior of *Tellinomya pectunculoides*, showing the hinge and adductor scars, enlarged twice—Ordovician (after Hall); C, Interior of the right valve of *Pectunculus subpilosus*—Tertiary; D, Interior of the valve of *Limopsis aurita*—Pliocene; E, Interior of *Macrodon Hirsonensis*—Jurassic.

oblique teeth, while the portion behind the beaks supports a few elongated teeth which run nearly parallel with the cardinal margin. Forms of this type are not uncommon in the Secondary rocks, but the earliest representatives appear in the Devonian rocks, and a single species exists at the present day. The sub-genus *Parallelodon* is very closely allied to *Macrodon*, possessing the same elongated posterior teeth directed parallel to the hinge-line, but the anterior teeth are also sub-horizontal. The species of this type are principally Carboniferous and Permian.

In the genus *Pectunculus* (fig. 583, C), the shell is nearly round and almost equilateral; the beaks are separated by a striated ligamental area of triangular form; the hinge-line is *curved;* and the hinge-teeth are oblique and form a semicircular row. *Pectunculus* is a comparatively modern genus, and does not seem to have come into existence before the Cretaceous period. Numerous species are known in the Tertiary rocks, and there are about sixty living types of the genus.

Limopsis, ranging from the Trias to the present day, has an orbicular, but slightly oblique shell (fig. 583, D), with a central triangular cartilage-pit, and a row of transverse teeth on each side of this. Lastly, the Miocene and Pliocene genus *Nuculina* has the shell oval or subtrigonal, with the anterior side abbreviated; the hinge-line being curved, and carrying a row of short transverse teeth completed posteriorly by one elongated lamelliform lateral tooth.

In connection with the present family we may consider the extinct genera *Cardiola* and *Cyrtodonta*, with some forms allied to the last of these, the precise affinities of these being uncertain. In the genus *Cardiola* (fig. 584) the shell is thin, equivalve, and oblique, with convex valves and prominent incurved beaks, and having the surface adorned with radiating grooves, which are crossed by concentric furrows in such a way as to give rise to radiating rows of tubercular eminences. There is a large triangular, transversely-grooved ligamental area below the beak, and the hinge-line is straight; but teeth have not been certainly detected in the typical forms of the genus, and the muscular impressions are unknown. Numerous species of the genus have been recognised in the Silurian and Devonian rocks, a characteristic species from the former system being the well-known *Cardiola interrupta*.

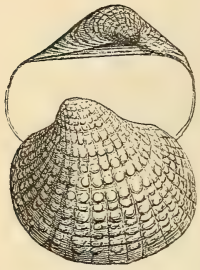


Fig. 584.—*Cardiola cornucopiæ*, from the Devonian rocks of Germany, of the natural size. (After Zittel.)

The shells of the genus *Cyrtodonta* (*Palæarca* of Hall) are ventricose and very inequilateral, the umbones being anterior (fig. 585). The hinge-area is undefined, and the surface is generally smooth. There are a few (three) anterior cardinal teeth, and "two or three remote oblique posterior teeth parallel to the hinge-margin" (Salter). The species of *Cyrtodonta* appear to be exclusively confined to the Ordovician, Silurian, and Devonian rocks, but the genus is said to occur in the Upper Cambrian. *Vanuxemia* comprises forms of the genus with nearly terminal beaks. In the genus *Megalomus*, again (fig. 586), are comprised forms essentially similar to *Cyrtodonta* (possibly identical with it), but having an excessively thickened and massive shell, which is usually strongly inflated. The valves are equal; the beaks strongly incurved and placed anteriorly; the hinge-line furnished with three or four (?) strong transverse teeth; and the anterior muscular impression extremely deep. The forms of this genus appear to be confined to the Silurian rocks, and often attain a great size, but they usually occur in the state of casts only.

Family 2. Nuculidæ.—This family comprises a number of marine Bivalves, in which the mantle-lobes may be open, or siphons may be

present, while the foot is discoid, and there are two nearly equal adductors. The shell is equivalve, with an internal or external ligament, but without a ligamental area; and the hinge is furnished with numerous narrow teeth. The pallial line may be entire or sinuated. This family includes two related groups, typified respectively by *Nucula* and *Nuculana* (*Leda*), the former group being characterised by the fact that the pallial line is entire and the posterior

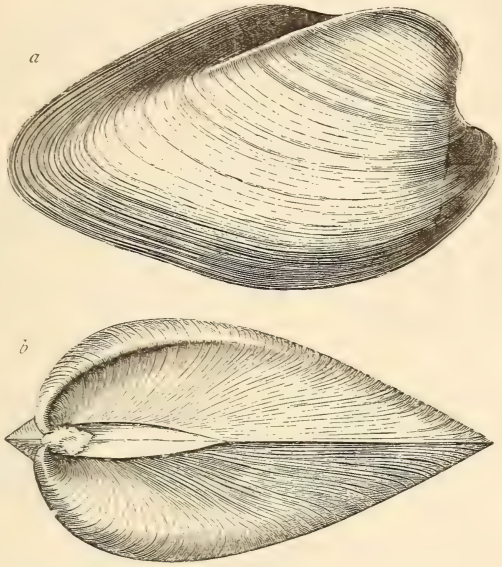


Fig. 585.—*Cyrtodonta Hindi*. (Billings.) Ordovician. *a*, Side view; *b*, Dorsal view.

side of the shell is short, while in the latter the pallial line is more or less sinuated and the posterior side of the shell is long.

In the genus *Nucula* itself (fig. 587) the shell is trigonal or oval, and the beaks are reversed and turned towards the posterior side of the shell, which is also the shortest side. The interior of the shell is nacreous and the ventral margin may be smooth or finely denticulated. The hinge is angulated, and shows a central internal cartilage-pit, flanked on each side by numerous teeth. The Secondary and Tertiary rocks have yielded a considerable number of species of *Nucula*, and there are many living forms. The Palæozoic shells which have been referred to *Nucula* probably belong really to other types (*Tellinomya*, &c.)

In the neighbourhood of the preceding may be placed the Silurian and Devonian genus *Cucullella* (fig. 589, B), in which the hinge-line is straight

or slightly curved, and the hinge is essentially similar to that of *Nucula*, except that the ligament is external; but there exists a long internal septum, which extends from below the beak towards the anterior muscular impression. The genera *Cleidophorus* (Ordovician and Silurian) and *Redonia* (Cambrian and Ordovician) appear to be related to *Cucullella*,

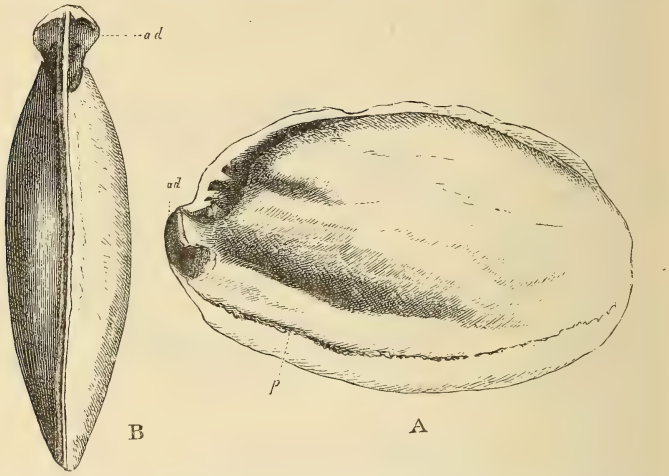


Fig. 586.—*Megalomus compressus.* A, Side view of the cast of the shell, natural size; B, The same viewed from above: *ad*, Cast of the adductor impression; *p*, Pallial line. (Original.)

since both possess a vertical internal plate, which commences in front of the beaks, and is continued downwards behind the anterior adductor, a deep slit being left in the cast of the shell by its removal.

Also in the neighbourhood of *Nucula* may be placed the genus *Tellinomya* (= *Ctenodonta*, Salter), though this type shows decided

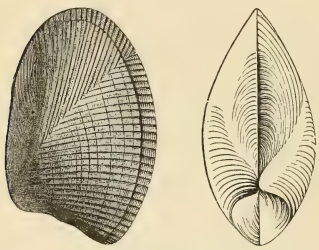


Fig. 587.—*Nucula bivirgata.* Gault.

Fig. 588.—*Tellinomya contracta.* Ordovician. *a*, Interior of right valve; *b*, Exterior of the same.

affinities with *Pectunculus* among the *Arcidæ*. In *Tellinomya* (figs. 583, B, and 588) the posterior side of the shell may or may not be the shortest, and the ligament is external, and is not placed, as in

Nucula, in an internal pit. The shell is generally oval or elongated, smooth, or marked with fine concentric lines; there is no ligamental area (as there is in *Pectunculus*), but the hinge carries numerous small transverse teeth. The species of *Tellinomya* range from the Ordovician to the Carboniferous, and the forms placed by Hall under the genus *Palæoneilo* are probably congeneric with the above.

The genus *Nuculana* (*Leda*) is the type of another group of the present family, which is distinguished by the fact that the shell is more or less produced posteriorly, and also usually by a more or less marked sinuation of the pallial line (589, A); for which reasons these forms are sometimes considered as constituting a separate family (*Nuculanidæ*). In *Nuculana* (*Leda*) the shell (fig. 589, A)

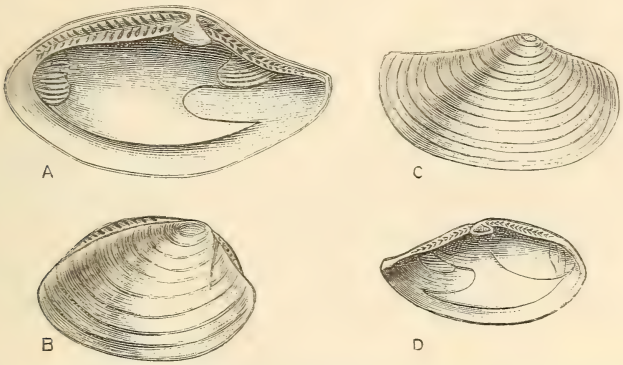


Fig. 589.—Types of *Nuculidæ*. A, Interior of the right valve of *Nuculana* (*Leda*) *lanceolata*—Pliocene; B, *Cucullella ovata*—Silurian; C, *Yoldia striatula*—Cretaceous, enlarged; D, Interior of the left valve of *Yoldia myalis*—Pliocene.

resembles that of *Nucula*, but is rounded in front and produced behind, while the pallial line is generally more or less indented. The hinge has numerous small teeth on either side of a small central cartilage-pit. Various species of the genus have been described from the Palæozoic rocks, beginning in the Devonian, and it is abundantly represented in the Secondary, Tertiary, and Post-Tertiary deposits, as well as by living forms. *Yoldia* (fig. 589, C and D) resembles the preceding in most respects, but the teeth are comb-like, and there is a large pallial sinus. The genus is perhaps represented as early as the Devonian or Carboniferous, but can hardly be distinguished from *Nuculana* in the fossil condition.

In the neighbourhood of *Nuculana* may be placed the Ordovician genus *Lyrodesma*, in which there is an equivalve oblique shell, truncated posteriorly, with an external ligament, and having a hinge of several

transverse teeth radiating in a fan-shaped manner from the beak (fig. 583, A). The Ordovician genus *Actinodonta* only differs from *Lyrodesma* in having a longer hinge-line, and in the fact that the central hinge-teeth are short or obsolete.

Order V. Submytilacea.

This order is defined by Fischer as comprising marine or fresh-water Bivalves, in which the mantle-lobes are free, with thickened margins; the foot may or may not be byssiferous, and there are (except in *Mülleria* only) two adductor muscles. The shell is almost always equivalve, the interior of the valves sometimes nacreous, sometimes not; the hinge is furnished with teeth, which are differentiated into a "cardinal" and two "lateral" series; the ligament is external; and the pallial line is simple. Dr Fischer includes in this order a number of families, of which the most important are the *Modiolopsidæ*, *Trigoniidæ*, *Unionidæ*, *Cardiniidæ*, *Carditidæ*, *Astartidæ*, and *Crassatellidæ*.

Family 1. Modiolopsidæ.—In this family the shell is equivalve and very inequilateral, the beaks being placed subterminally towards the anterior end of the shell. There are two adductor impressions, of which the anterior is smaller than the posterior, and the pallial line is entire. The ligament is external, and the hinge may or may not be furnished with teeth. The principal genus of this family is *Modiolopsis* itself (fig. 590), in which the shell is elongated, re-

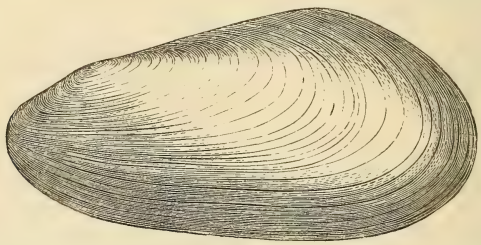


Fig. 590.—*Modiolopsis modiolaris.* Ordovician.

sembling that of a *Modiola* in shape, with anterior beaks, and having the surface smooth, or marked by fine concentric lines of growth. The posterior end of the shell is broader than the anterior; the hinge-line is long and nearly straight, and there is a long ligamental groove extending to the posterior extremity, no teeth being apparently developed. The impression of the anterior adductor is small but deep, that of the posterior adductor being wide and ill-defined. The species of *Modiolopsis* are Ordovician and

Silurian. The Devonian genus *Modiomorpha* is closely related to *Modiolopsis*, but the left valve has a single cuneiform tooth, which fits into a corresponding cavity in the right valve.

Family 2. Trigoniidæ.—The members of this family are marine, with a large bent foot, which does not secrete a byssus, and with free mantle-lobes. The shell (fig. 592) is equivalve, subtrigonal, nacreous internally, with an external ligament placed behind the beaks, and a simple pallial line. The hinge-teeth are few in number (fig. 591), varying from one to three in each valve. The only living genus in this family is *Trigonia* itself, but various extinct types may be associated with this.

In the genus *Trigonia* (figs. 591-593) the shell is thick, nacreous internally, trigonal in shape, and very inequilateral, the beaks being

Fig. 591.—Interior of the left valve of *Trigonia pectinata*. Recent. *f f*, Hinge-line, with teeth and sockets; *a*, Anterior adductor impression; *a'*, Posterior adductor impression.

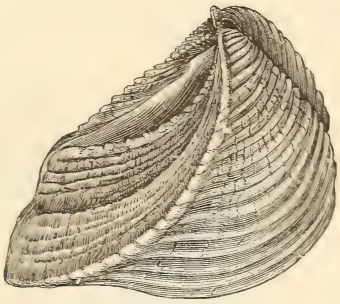


Fig. 592.—*Trigonia costata*, from the Jurassic rocks.

directed backwards. The anterior side of the shell is rounded, and the posterior side is produced and obliquely truncated, constituting a special "area," which is often ornamented differently to the rest of the shell, from which it is divided off by a more or less pronounced ridge running from the beak to the hinder margin. The so-called "escutcheon" is a smaller area, which is cut off from the rest of the shell by a second oblique ridge running close to the dorsal margin of the shell behind the beaks. The hinge of the right valve is furnished with two diverging teeth, the faces of which are strongly striated; while that of the left valve has a strong central tooth, striated on both sides, and two lateral, externally striated teeth. The surface of the shell is rarely almost smooth, the majority of species exhibiting a characteristic ornamen-

Fig. 593.—*Trigonia scabra*. Chalk.

tation, consisting sometimes of concentric lines, but more usually taking the form of radial rows of tubercles or diverging ribs. By the form of the shell and the ornamentation of the surface the species of *Trigonia* may be divided into a number of minor groups. The earliest types of *Trigonia* appear in the Lias, and the genus exhibits an extensive development in the later Jurassic and Cretaceous formations. A few Tertiary species are known, and the Australian seas are inhabited by five existing forms.

The Triassic genus *Myophoria* (fig. 594) comprises sub-triangular shells, obliquely keeled, smooth, concentrically striated, or with a partial development of radiating ribs. The left valve has three, and the right two, cardinal teeth. In the genus *Schizodus* (= the *Axinus* of many authors, but not of Sowerby) are comprised a number of Carboniferous and Permian Bivalves, in which the shell (fig. 595) is obliquely ovate, and is in many respects externally

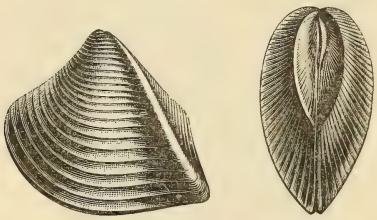


Fig. 594.—*Myophoria lineata.* Trias.

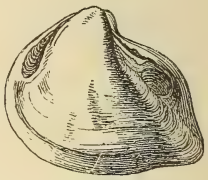


Fig. 595.—Cast of *Schizodus obscurus*, from the Permian rocks, of the natural size. (After Zittel.)

similar to *Myophoria*, except that the surface is smooth and non-plicate, while the posterior side is bounded by an obscure oblique ridge, and is not markedly angular. The right valve has two diverging teeth, and the left valve has a strong central tooth, with a smaller marginal tooth on each side. The Devonian genus *Curtonotus* and the Carboniferous *Dolabra* may be provisionally associated with the present family.

Family 3. Unionidæ.—In this family the foot is large and compressed, not byssiferous except in the fry; the mantle-lobes are more or less free, being usually united between the siphonal apertures; and there are two adductor muscles. The shell is ordinarily equivalve, nacreous internally, with a thick epidermis, and a large external ligament. The hinge may be edentulous or furnished with well-developed teeth, and the pallial line is entire. All the members of this family are inhabitants of fresh water, and they are, therefore, not known in the fossil condition except in fluviatile and lacustrine deposits. If *Anthracosia* and *Carbonicola* be removed to the *Cardiniidæ*, the genera *Unio* and *Anodonta* are the only types of this family which need consideration here.

The shell in the genus *Unio* (fig. 596) is generally oval or elongated, the beaks being placed towards the anterior end, and a prominent external ligament being present. The surface is smooth, concentrically striated, or in some cases ribbed, and is covered with a thick horny epidermis, which is often destroyed over the beaks. The hinge of the right valve has two anterior lateral teeth, and a long laminar posterior lateral tooth; while that of the left valve has a single anterior lateral tooth, a cardinal tooth, and two laminar posterior lateral teeth. The most ancient fossil representatives of the River-mussels appear in the Purbeck beds (Upper Jurassic), and other forms (*Unio Valdensis*, &c.) are found in the Wealden deposits. A considerable number of Tertiary types of *Unio* have been recognised, principally in the Miocene beds, but the genus attains its maximum at the present day.

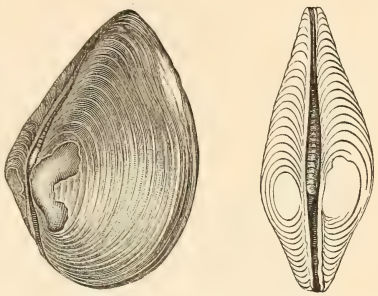


Fig. 596.—*Unio Valdensis*. Wealden (Lower Cretaceous).

The genus *Anodonta* or *Anodon* comprises the living Swan-mussels, and is distinguished from *Unio* by the tenuity of the shell and the edentulous character of the hinge. The shell forms an elongated oval, compressed in the young condition but convex when old, with anteriorly placed beaks; and it often attains a considerable size. The earliest undoubted fossil forms of this genus appear in the Eocene Tertiary; but the Upper Devonian rocks of Ireland and Scotland have yielded the remains of a large Bivalve which has been referred here under the name of *Anodonta* (*Archanodonta*) *Jukesi*.

Family 4. Cardiniidæ.—This family was proposed by Zittel to include a number of Bivalves, in which there is an equivalve, oval, or trigonal shell, which is not nacreous internally, and in which the surface is smooth or concentrically striated. The ligament is external, the pallial line is entire, and the muscular impressions are deep and simple. The cardinal teeth are generally small, but the lateral hinge-teeth are more or less developed, and are often very thick. The forms included in this family are all extinct, and present relationships on the one hand to the *Unionidæ* and on the other hand to the *Astartidæ*. From the fossils with which they are associated, they would appear to have been marine, or to have inhabited brackish waters.

In the genus *Cardinia* (fig. 597, B) the shell is trigonal or ovate,

very inequilateral, posteriorly attenuated, and not ventricose. The ligament is external, in a deep furrow, and the cardinal teeth are feebly developed or wanting, while there is a single prominent lateral tooth on each side. The surface is smooth or concentrically striated, and the beaks are not eroded. The genus is extinct, and is confined to the Triassic and Jurassic rocks. *Trigonodus*, of the Trias (fig. 597, c), is closely allied to *Cardinia*, but the cardinal

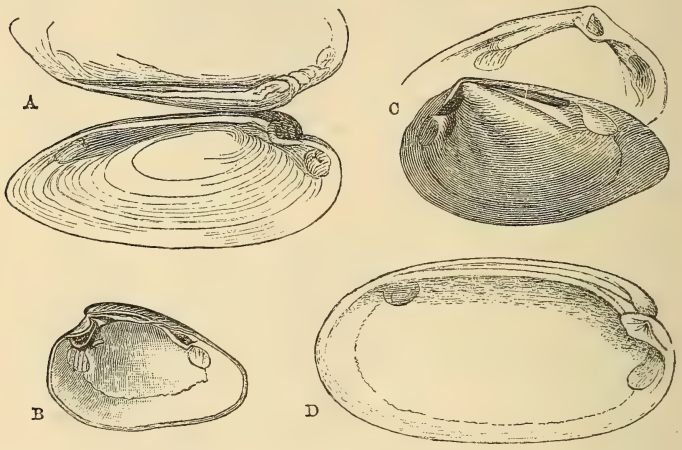


Fig. 597.—Types of *Cardiniidæ*. A, *Anthracosia Lottneri*, from the Coal-measures of Germany; B, Interior of the right valve of *Cardinia Listeri*, Jurassic; C, Cast of the interior and hinge-line of *Trigonodus Sandbergi*, from the Trias of Würtemberg; D, Interior of the left valve of *Guerangeria Davousti*, from the Inferior Devonian of France. (After Zittel, Œhlert, and Woodward.)

teeth are more fully developed, the right valve having one and the left valve two. Various Palæozoic shells have been referred to *Cardinia*, but the true affinities of these are doubtful.

We may place in this family the Devonian and Carboniferous genus *Carbonicola*, comprising Unionoid Bivalves, with thick shells, an external ligament, and a concentrically-striated surface. The beaks are not eroded; and the hinge has a thick cardinal tooth in the right valve, with a long lamellar lateral tooth on each side.

The genus *Anthracosia* comprises a number of thin-shelled Bivalves in which the shell is long-oval and inequilateral (fig. 597, A), and the surface is smooth or concentrically-striated. The ligament is external, and the hinge seems to have been provided with a single cardinal tooth in each valve, without lateral teeth. The *Anthracosiæ* are found in abundance in parts of the Coal-measures and Lower Permian series, and they may perhaps have been inhabitants of brackish water.

Lastly, we may place here the Lower Devonian genus *Gueran-*

geria, of Œhlert, in which the shell (fig. 597, D) is long-oval and very inequilateral, with small subterminal beaks, and a concentrically-striated surface. The ligament is external; both valves have an elongated posterior lateral tooth; and the right valve has a cardinal tooth which fits into a corresponding socket in the left valve.

Family 5. Carditidæ.—In this family the mantle-lobes are free, the foot is byssiferous or is grooved inferiorly, and there are two adductor muscles. The shell is equivalve, solid, cordate, oval, or transversely elongated, and generally adorned with radiating ribs. The pallial line is entire; the ligament is almost always external; and the hinge is massive, and supports one or two oblique cardinal teeth and sometimes lateral teeth as well. The members of this family are marine in habit, and the two most important recent genera are *Venericardia* and *Cardita*, which are closely related to one another, and are separated principally by characters connected with the living animal, the former having a large foot which is grooved and non-byssiferous, while in the latter the foot is short and secretes a byssus.

In both *Venericardia* and *Cardita* the shell (fig. 598) is massive, more or less cockle-shaped, inequilateral, and adorned with radiat-

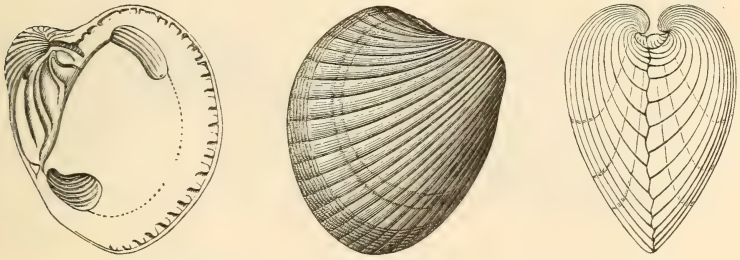


Fig. 598.—*Venericardia* (*Cardita*) *planicosta*. Eocene Tertiary.

ing ribs, the ventral margin being denticulated or crenulated. The ligament is external, and the hinge-plate is thick and furnished with powerful cardinal and variably developed lateral teeth. The genus *Cardita* ranges in time from the Trias to the present day; while the species of *Venericardia* abound in the Cretaceous and Tertiary rocks, and a few forms still survive.

With the preceding may be associated, provisionally at any rate, a number of wholly extinct genera. Of these the genus *Pleurophorus* (fig. 599) possesses an oblong shell, with anterior, almost terminal beaks, and a massive hinge. Each valve has two diverging cardinal teeth, with a single elongated lateral tooth placed posteriorly; and the anterior adductor impression is very deep,

and is bounded behind by an elevated ridge. The species of *Pleurophorus* range from the Devonian to the Trias, but they are most characteristic of the Permian formation. Possibly allied to the above is the *Matheria* of the Ordovician rocks of Canada, in which the beaks are placed anteriorly and the ligament is external; and the Silurian genus *Anodontopsis* may, perhaps, also find a place here.

Fig. 599. — Interior of the left valve of *Pleurophorus costatus*, from the Permian rocks. (After King.)

In this neighbourhood Dr Fischer likewise places the extinct genera *Myoconcha* and *Hippopodium*. In the former of these the shell is thick and mussel-shaped, with nearly terminal beaks, and having the ligament external and contained in a groove. The hinge is massive and curved, and in the right valve carries a single oblique tooth. The anterior adductor impression is deep, and the pallial line is entire. The species of *Myoconcha* are essentially characteristic of the Secondary rocks, though the genus has been stated to occur in the later Palæozoic deposits. In the genus *Hippopodium* (fig. 600) the shell is oblong, massive, and ventricose, with nearly terminal incurved beaks, an external

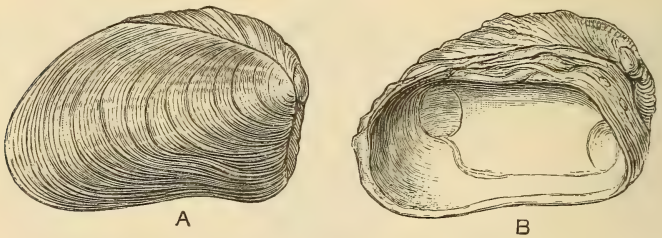


Fig. 600.—*Hippopodium ponderosum*. Lias.

ligament, and an entire pallial line. The hinge carries in each valve an oblique tooth, which becomes obsolete with age. The genus is confined to the Jurassic rocks, a familiar species being the *Hippopodium ponderosum* of the Lias.

Family 6. Astartidæ.—In this family the mantle-lobes are free, and the foot is long and pointed. The shell is equivalve, thick, trigonal or oval, with a more or less distinct "lunule." The ligament is external, and the hinge thick, with two or three cardinal teeth in each valve, the lateral teeth being obsolete. There are two adductor impressions, of which the anterior is the deepest, and the interior of the shell is not pearly. The members of this family are all marine, and the principal genera are *Astarte* and *Opis*.

In the genus *Astarte* (fig. 601) the shell is thick, and usually concentrically furrowed, subtrigonal, rounded, or oval in form, inequilateral, and usually with a well-marked "lunule." The ligament is external, and there are two cardinal hinge-teeth in each valve, the front tooth of the right valve being large and thick. The genus *Astarte* is stated to occur in the Palæozoic series, from the Silurian onwards; but the affinities of the supposed ancient representatives of this type are uncertain. From the Mesozoic deposits numerous species of *Astarte* have been obtained, and the genus attained its maximum development at this period. The Tertiary species are fewer in number, and about a score of living species are known. The Carboniferous genus *Astartella* and the *Cypricardella* (*Microdon*) of the Devonian and Carboniferous rocks appear to be related to *Astarte*. The genus *Pachydomus*, of the Devonian rocks of Australia and Tasmania, may, perhaps, also be placed in this family.

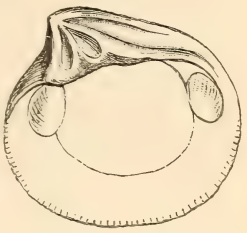


Fig. 601. — Interior of the right valve of *Astarte detrita*. Jurassic.

Fig. 602.—Interior of the right valve of *Opis lunulata*. Jurassic.

Of the remaining genera of the *Astartidæ*, the only one which need be specially noticed is *Opis*, of which numerous species are found in the Triassic, Jurassic, and Cretaceous rocks. In this genus the shell (fig. 602) is heart-shaped and keeled, with prominent incurved beaks, a distinct lunule, and a single cardinal tooth in each valve.

Family 7. Crassatellidæ. — The general characters of the animal in this family are similar to those in the *Astartidæ*.

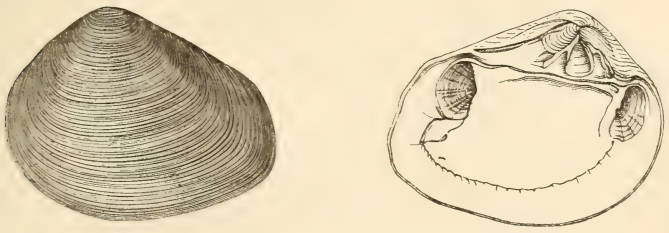


Fig. 603.—*Crassatella ponderosa*. Eocene Tertiary.

The shell also agrees with that of the *Astartidæ* in being equivalve, massive, and subtrigonal, with a distinct "lunule." The shell is, however, more or less produced posteriorly, and the ligament is lodged in an internal groove. The type of this family is *Crassatella* itself (fig. 603), in which the shell is thick, solid, and

ventricose, attenuated posteriorly, and having a concentrically furrowed surface. There is a distinct "lunule," and the hinge is broad, with strong cardinal teeth and feebly developed lateral teeth, while there is a well-marked pit in the hinge-plate of each valve for the reception of the internal ligament. The genus is marine; the earliest forms appearing in the Cretaceous rocks, while numerous Tertiary and about thirty-five Recent species are known. The Cretaceous genus *Crassatellina* has been associated with *Crassatella*, but it agrees with the *Astartidæ* in having an external ligament.

Order VI. Erycinacea.

This order is defined by Fischer as comprising marine Bivalves, with a byssiferous foot, and without respiratory siphons, but with the exceptional character that the branchial aperture is placed anteriorly, in front of the pedal opening, instead of being placed posteriorly below the exhalant or anal aperture. The shell is small and thin, equivalve, free, the hinge being toothed or toothless, and an internal cartilage-pit and generally an external ligament being present. There are two adductors, and the pallial line is entire. This order includes the two small families of the *Erycinidæ* and *Galeommidæ*.

Family 1. Erycinidæ.—The shell in this family is small and thin, oval or trigonal in form, equivalve, mostly inequilateral, and smooth or finely striated. The hinge carries one or two cardinal teeth, but lateral teeth are not constant. The internal ligament is contained in an oblique groove between the hinge-plates of the valves, and the external ligament is feebly developed.

The genus *Erycina* includes a large number of small shells which are found in Tertiary deposits, and are specially abundant in the Eocene rocks. A single species has been described from the Cretaceous rocks of North America. Very closely related to *Erycina*, if generically separable from it, is the genus *Kellia*, which is not known in the fossil condition (as distinct from the preceding). Related genera are *Lepton* and *Montacuta*, both of which are known by Tertiary forms, and still survive.

Family 2. Galeommidæ.—In this family the shell is small, thin, equivalve, and subequilateral, and is more or less gaping. The hinge may be edentulous, or may be provided with one or two teeth; and the ligament is internal, and is lodged in a median pit. All the forms included in this family are marine, the two principal genera being *Galeomma* and *Scintilla*, both of which are represented by living forms. The oldest species of *Galeomma* are found in the Pliocene deposits, while *Scintilla* appears as early as the Eocene.

Order VII. Cardiacea.

The Lamellibranchs included in this order are inhabitants of the sea or of brackish water, and possess a byssiferous or grooved foot; while there are two adductor muscles. (According to the views of

some malacologists, *Tridacna* is monomyary.) The shell is equivalve and thick, the hinge with or without teeth, the ligament external, and the pallial line simple or slightly indented. This division includes the two principal families of the *Tridacnidæ* and *Cardiidæ*.

Family 1. Tridacnidæ.—In this family the shell is equivalve, thick, not nacreous internally, and usually truncated or gaping in front, the ventral margin being undulated or dentate, and the surface ribbed. The hinge has a single cardinal tooth and one or two posterior lateral teeth in each valve, and the ligament is external. The foot is finger-like and usually secretes a byssus; the mantle-lobes are extensively united; and the impressions of the adductors are blended together and are subcentral in position. (According to some authorities, the anterior adductor is really absent.)

In the genus *Tridacna* itself (fig. 604) the shell is massive, of large size, and subtrigonal in form; and there is a wide byssal aperture just in front of the beaks. On the other hand, in the closely

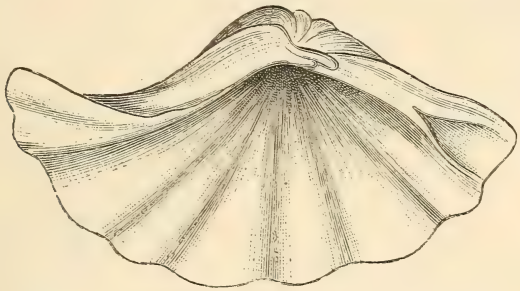


Fig. 604.—*Tridacna media.* Tertiary. Interior of right valve.

allied *Hippopus* the shell is closed, and the pedal aperture is only indicated by small serrations of the margin of the valves. *Tridacna* is only known in a fossil condition by a few species from the later Tertiaries. The Palæozoic *Eurydesma* has also been referred to this family.

Family 2. Cardiidæ.—In this family are included the "Cockles," in which the mantle is open in front to allow of the passage of a large and sickle-shaped foot, while it is closed behind and gives origin to two longer or shorter siphons. The shell is equivalve and is not nacreous, usually heart-shaped in form, with radiating ribs, and with the ventral margin toothed or wavy. The ligament is external, and the hinge carries one or two cardinal teeth in each valve, usually with lateral teeth as well. There are two adductor-muscles, and the pallial line is entire or slightly indented.

In the genus *Cardium* are comprised the true Cockles, in which the shell is ventricose, the beaks pronounced, and placed nearly in

the centre of the dorsal margin, the margins crenated, and the pallial line more or less indented. The surface is adorned with radial ribs or striæ, which often carry spines. A very large number of recent species of *Cardium* are known, and between three and four hundred fossil forms have been referred here. Certain Palæozoic types have been placed under this head, but the affinities of these are doubtful. On the other hand, the genus is largely represented by undoubted types throughout the Mesozoic and Kainozoic series. The genus *Cardium* has been broken up into numerous minor groups, most of which can be with difficulty, or not at all, recognised in the fossil condition. *Papyridea*, *Lævicardium*, and *Lithocardium* are Secondary to Recent types closely allied to *Cardium* proper. *Protocardia* (fig. 605) has the posterior slope of the shell radiately ribbed, while the rest of the shell is concentrically striated. *Hemicardium* has keeled valves, the shell appearing cordate as viewed from behind or in front. *Lymnocardium* and *Adacna* include brackish-water and fresh-water Cockles, in which the cardinal teeth are small or obsolete; and the species of the former are common in some of the fluviatile and estuarine deposits of the Upper Tertiary period. The recent species of *Adacna* are found abundantly in the Black Sea and Caspian Sea, and in the Sea of Aral, often in quite brackish water, and the fossil species are extraordinarily plentiful in the Tertiary deposits of Austria, Hungary, and Southern Russia. The genus is remarkable for the exceeding variability of the hinge as regards the number of teeth. *Byssocardium*, again, includes Eocene and Miocene Cockles, in which the shell is truncated anteriorly, and possesses a large byssal sinus.

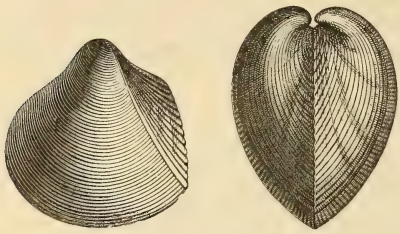


Fig. 605.—*Cardium* (*Protocardia*) *Hillanum*. Upper Greensand.

The most remarkable of the early types of the *Cardiidæ* is the genus *Conocardium* (= *Pleurorhynchus*), which ranges from the Ordovician to the Carboniferous, but is specially characteristic of the Devonian and Carboniferous formations. The shell in this genus (fig. 606) is keeled, and very oblique, the *anterior* end (sometimes regarded as the posterior end) of the shell being short and abruptly truncated, so as to appear as a cordate flattened area when the shell is viewed from the front. Just below the beaks the shell is produced anteriorly into a long cylindrical tubular projection or beak. *Posteriorly* the shell is elongated and contracted, the valves being widely deficient or gaping at the extremity. The hinge-line

is long and straight; and two cardinal teeth, with a hinder lateral one, appear to be present.

Family 3. Lunulicardiidæ.—This family is one of very uncertain value, and embraces only the imperfectly understood genus *Lunulicardium* of Münster. In this genus the shell is obliquely oval, equivalve, and inequilateral, the surface being adorned with radiating ribs. The anterior end of the shell is truncated, and the pos-

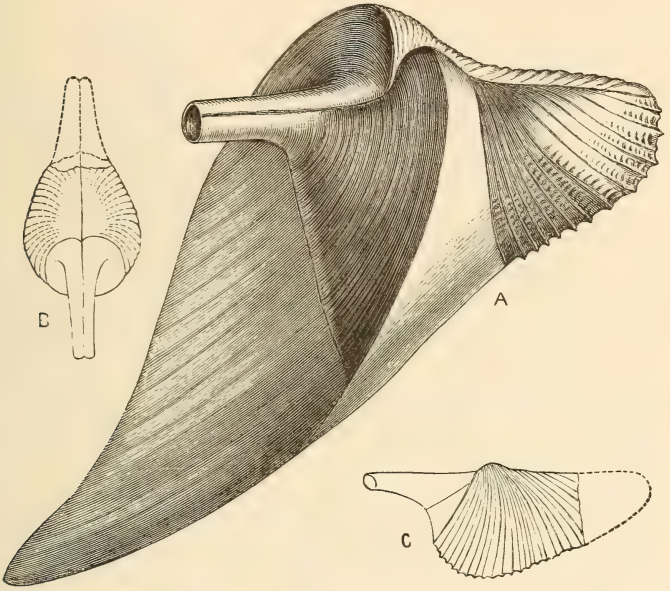


Fig. 606.—A, *Conocardium giganteum*, showing the truncate anterior and produced posterior end of the shell, with the tubular prolongation of the former; B, *Conocardium inflatum*, viewed from above: C. The same viewed laterally. Carboniferous. (After M'Coy.)

terior end is sub-alate. The cardinal line is "marked by a lunate hiatus in each valve, which was probably occupied by the ligament" (Hall). The hinge and muscular markings are unknown. In this genus, as in *Conocardium*, the truncated end of the shell is sometimes regarded as the *posterior* end. The species of *Lunulicardium* are found in the Silurian and Devonian rocks, being very abundant in the Silurian rocks of Bohemia.

Order VIII. Chamacea.

In this order, represented at the present day by the single genus *Chama*, the mantle is closed, the mantle-cavity communicating with the exterior by apertures for the foot and for the in-going and out-

going currents of water; and the foot is rudimentary. The shell is irregular, very inequivalve, always attached to foreign objects by the substance of one valve. In structure, the shell is thick, and consists of an internal porcellanous and an external prismatic layer, often with special and remarkable modifications in particular types. The hinge is thick, and is provided with cardinal teeth, but lateral teeth are wanting. The ligament may be external or internal, or is wanting altogether. The pallial line is entire, and the two adductors leave well-marked scars, or may be inserted upon special internal calcareous septa. This order includes the two families of the *Chamidæ* and the *Rudistæ*.

Family 1. Chamidæ.—In this family the shell is inequivalve, and is generally attached to foreign objects by the substance of one of the valves. The ligament is normally external, and lies in a deep groove, but it may become more or less completely concealed from view. The hinge is massive, and usually carries two teeth in one valve and one in the other. The adductor impressions are very large, and the pallial line is entire. The family includes the single recent genus *Chama*, together with a number of exceedingly remarkable Mesozoic Bivalves, such as *Diceras*, *Requienia*, *Monopleura*, *Caprina*, *Caprotina*, &c. The structure of these latter is, however, so complicated that they cannot be advantageously treated of here except in an exceedingly brief manner; since a full understanding of their characters can only be obtained by the examination of actual specimens.

In the genus *Chama* (fig. 607) the shell is attached to foreign objects by the beak of the left valve, or, more rarely, by that of the right valve. The beaks of both valves are incurved and are directed anteriorly. The free valve is the smallest, and the surface of both valves is furnished with foliaceous expansions, derived from a thick external prismatic layer, below which is situated an internal porcellanous layer. The massive hinge usually carries a single tooth in the free valve, articulating with two teeth in the attached valve. The recent species of *Chama* are all inhabitants of the sea. The fossil species commence in the Cretaceous rocks, a number of forms being found in the Tertiary deposits.

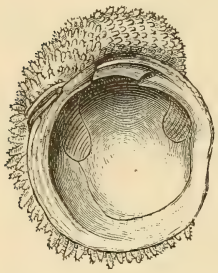


Fig. 607. — Interior of the attached valve of *Chama lamellosa*. Eocene Tertiary.

In the genus *Requienia* (fig. 608) the shell is exceedingly inequivalve, the right valve being small, subspiral, and operculiform, while the left valve is of large size and is spirally rolled up, its beak serving for the attachment of the shell to some foreign body. The ligament is external,

and is prolonged on the outside of the left valve to its beak; and the hinge is edentulous or has a single tooth. The genus is distinguished from *Chama* by its generally smooth or striated surface, and the want of the foliaceous expansions of the latter. The species of *Requienia* are exclusively confined to the Cretaceous period.

In the genus *Diceras* (fig. 609) the shell is slightly inequivalve, the beaks being very prominent and spirally rolled up in both valves.

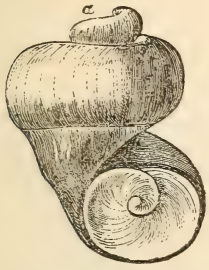


Fig. 608. — *Requienia ammonia*, one-fourth of the natural size. *a*, Point of attachment. Cretaceous rocks. (After Woodward.)

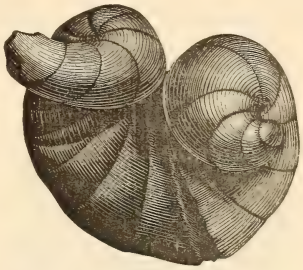


Fig. 609.—*Diceras arietina*. Upper Jurassic.

Either the right or the left valve may be the largest, and in that case serves for the attachment of the shell to foreign bodies by means of the umbo. The ligament is external, and is prolonged to the apices of the beaks in external furrows. The hinge is very thick, with prominent teeth (two in one valve and one in the other); and the muscular impressions are bounded by long spiral ridges. The species of *Diceras* are exclusively confined to the Middle and Upper Jurassic rocks, abounding especially, in some regions, in beds of the age of the Coral-rag of Britain.

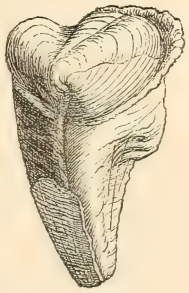


Fig. 610.—*Monopleura trilobata*, of the natural size, viewed from behind. Cretaceous rocks.

In the genus *Monopleura* (fig. 610) the shell is very inequivalve, and is fixed by the apex of the right valve, which is the larger of the two, and is conical in form, being either straight, or more or less spirally inrolled. The left valve is small, and either flat or widely conical, with a submarginal umbo. The ligament is prolonged externally in grooves, which run to the beaks in each valve. The surface is generally radially striated. The species of this genus are wholly confined to the Cretaceous rocks, and principally characterise the lower division of this formation. Closely allied to *Monopleura*, and also confined to the Cretaceous rocks, is the genus *Caprotina*.

Here also must be placed the remarkable Cretaceous genera *Caprina*, *Plagioptychus* (= *Caprina* in part), and *Ichthyosarcolites* (= *Caprinella* and *Caprinula*), in all of which the shell (fig. 611) is very inequivalve, thick-walled, and either fixed by the apex of the right valve, or, in some cases, free. In all these forms the shell-structure consists of a thin external prismatic layer, and a greatly developed internal laminated or porcellanous layer, the laminæ of which may be more or less extensively separated by vacant spaces (the so-called "water-chambers"). In the substance of the left valve in these genera there is, further, developed a

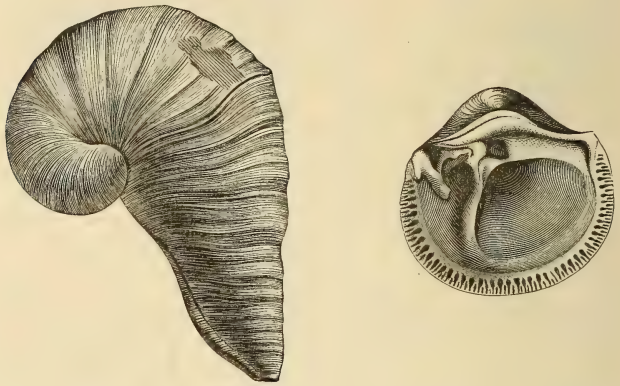


Fig. 611.—*Plagioptychus* (*Caprina*) *Aguilloni*. The right-hand figure shows the interior of the left valve.

system of radial canals which run from the beak to the free margin of the valve, where they terminate in foramina, and which are sometimes simple and sometimes complex in their arrangement.

Family 2. Rudistæ (*Hippuritidæ*).—In this family the shell is very inequivalve (fig. 612), unsymmetrical, massive, the two valves being dissimilar in structure and sculpturing. The shell is attached by the apex of the elongated right valve, which is conical in form; while the left valve is depressed, often operculiform, and has a central umbo. There is no ligament; but the free upper valve is fixed into the conical lower valve by powerful teeth and processes, and is only capable of movement in a vertical direction. There are two large adductor impressions, those of the left valve being upon prominent apophyses. The pallial line is simple and submarginal.

The shell-structure in the *Hippuritidæ* is exceedingly peculiar, and has been described by Zittel as follows: "The *lower* valve consists of two layers, the outer of which is formed of perpendicular prisms having a direction parallel to the long axis of the shell, and intersected by numer-

ous transverse lamellæ, which are horizontal, or are directed somewhat obliquely outwards and upwards, the intersection of the two series giving rise to a lattice-like structure (fig. 614). The shell splits easily along the line of these transverse lamellæ, the upper surfaces of which—as also of the thickened upper margin of the shell—exhibit radially disposed vascular impressions. The inner stratum of the shell is white, porcellanous and laminated in structure. Sometimes the parallel lamellæ are separated by vacant spaces (fig. 613), thus giving rise to intervening lacunæ ('water-chambers'). This is especially the case in *Hippurites*, in which the greater portion of the conical lower valve is formed by the inner shell-layer. The two shell-layers separate readily from one another; and

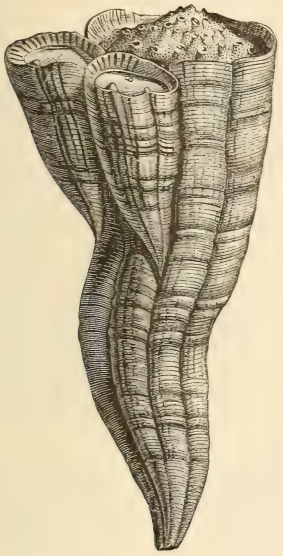


Fig. 612.—*Hippurites Toucasianus*. A large individual, with two smaller ones attached to it. Cretaceous.

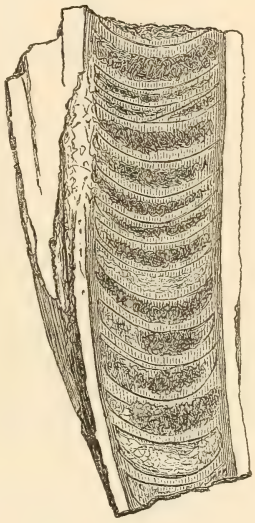


Fig. 613.—Vertical section of a broken shell of *Hippurites organisans*, without the body-chamber, showing the horizontal partitions and intervening spaces ("water-chambers"), of the natural size. (After Zittel.)

as the inner one, at least in *Sphærulites* and *Radiolites*, resists destruction during fossilisation less completely than the outer one, it commonly happens that only the outer layer is preserved, and the mould of the body-chamber appears to be separated from the latter by a vacant space. Still more commonly, the inner layer has undergone transformation, and has been replaced by crystalline calcite. The *upper* valve consists, like the lower one, of two layers, but the cellulo-prismatic outer stratum is mostly of small thickness, and in *Hippurites* is traversed by a complicated system of canals, while the inner porcellanous and laminated layer is frequently converted into crystalline calcite." It is usually supposed that the outer layer of the shell in the *Hippuritidæ* corresponds with the external prismatic layer in such Bivalves as *Pinna;* but it differs from the latter in the great size of the component prisms, and in the fact that

these are directed *parallel* to the surface of the shell instead of perpendicular to the surface. Moreover, the intersection of the prisms by horizontal or oblique lamellæ gives rise to an altogether unique vesicular structure. Further, the prisms in the outer shell-layer in the ordinary Bivalves are solid, whereas in the *Hippuritidæ* they are hollow, and were probably occupied in life by some organic infilling.

The shell of *Hippurites* (fig. 612) is inversely conical or cylindrical, and sometimes attains a length of two or three feet. The shell is attached by the larger conical valve, and is closed by a small depressed free valve, with a central umbo. In *Radiolites* the shell is inversely conical, bi-conical, or cylindrical, with dissimilar valves. The upper valve is sometimes flat, sometimes conical, and has a

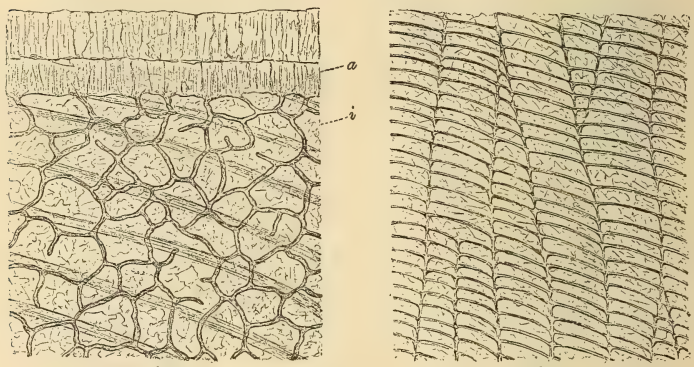


Fig. 614.—Minute structure of the shell of *Sphærulites* (*Radiolites*) *Mortoni*, from the Upper Greensand, Cambridge. A, Transverse section, enlarged ten times, showing the large hollow prisms of the outer layer (*i*) transversely divided, the thin inner layer (*a*) being converted into crystalline calcite; B, Vertical section, similarly enlarged, showing the prisms of the outer layer with their intersecting cross-partitions. (Original.)

central or lateral umbo. The external shell-layer in the lower valve is exceedingly thick, and is made up of hollow calcareous prisms, which run parallel with the surface and are intersected by close-set oblique transverse plates (fig. 614); while the inner shell-layer is comparatively thin. In the typical forms of *Radiolites* the lower valve commonly exhibits on one side two bands running from the beak to the upper margin, which are smooth or striated differently from the rest of the valve. In the closely allied genus *Sphærulites* these bands are wanting.

The *Rudistæ* are not only entirely extinct, but are exclusively restricted to rocks of Cretaceous age, being especially characteristic of the middle and upper divisions of this formation, particular types commonly being confined to special stratigraphical horizons. The Cretaceous deposits of Britain, Europe, Algeria, Asia Minor, Persia,

and North America have yielded the remains of these singular Molluscs; but they are especially abundant in Southern Europe, where they often give rise to great beds of marble ("Hippurite Limestones," "Rudisten-Kalk"). In all the *Rudistæ* the two valves of the shell are more or less conspicuously dissimilar in shape and size, and often in external sculpturing or internal structure. They appear to have lived in shallow water, and to have grown in great beds or banks, much as Oysters do.

Order IX. Conchacea.

In this order, the inhalant and exhalant openings of the mantle are usually prolonged into siphons; the foot may or may not be byssiferous; and there are two adductor muscles. The shell is equivalve, regular, and free; the ligament is almost always external; the hinge has cardinal teeth, generally with lateral teeth as well; and the pallial line is usually sinuated, but may be entire. The Bivalves included in this order are mostly marine, but sometimes inhabit brackish or fresh waters. The principal families included under this head by Fischer are the *Megalodontidæ*, *Cyprinidæ*, *Veneridæ*, *Cyrenidæ*, *Ungulinidæ*, *Unicardiidæ*, *Tancrediidæ*, *Donacidæ*, *Psammobiidæ*, and *Solenidæ*.

Family 1. Megalodontidæ.—In this family the shell (fig. 615) is equivalve, very thick, and mostly smooth or concentrically striated,

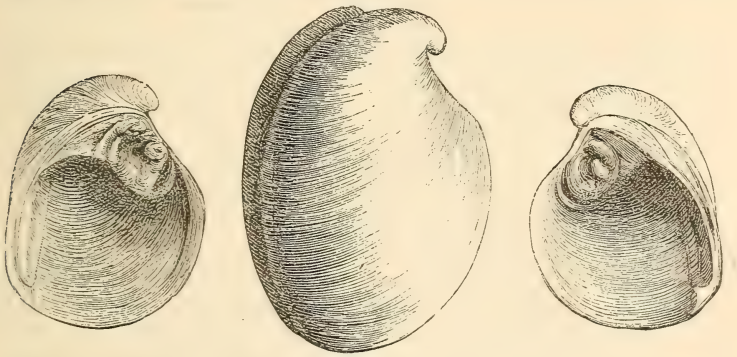


Fig. 615.—*Megalodon cucullatus*, from the Middle Devonian of Paffrath. (After Zittel.)

the beaks being turned to the anterior side of the shell. The hinge-plate is very broad, each valve carrying one or two strong cardinal teeth, with feebly developed lateral teeth. The ligament is external, and the posterior adductor impression is placed upon a more or less prominent ridge. All the genera of this family are extinct, the principal type being *Megalodon* itself. In this genus (fig. 615) the shell

is massive, with subspiral beaks and an external ligament. The right valve has two striated cardinal teeth, and the left valve has one, partially-divided cardinal tooth. The species of *Megalodon* range from the Devonian to the Trias, a familiar species being the *M. cucullatus* of the Middle Devonian rocks. Allied to the preceding is the Jurassic genus *Pachyrisma*, in which the shell is thick and ponderous, and the umbones are subspiral.

Family 2. Cyprinidæ.—In this family the mantle-lobes are united behind by a curtain pierced by two siphonal orifices, and the foot is thick and tongue-shaped. The shell is equivalve, thick, the beaks directed anteriorly and often inrolled, and the hinge is furnished with cardinal and lateral teeth. The ligament is external, and the pallial line is entire.

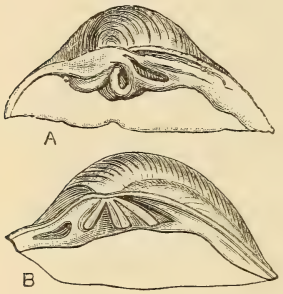


Fig. 616.—A, Hinge of *Cyprina tumida*, Pliocene; B, Hinge of *Cyprina Saussuri*, Cretaceous.

The principal genus in this family is *Cyprina* itself, in which the shell is large, strong, and rounded, with a thick epidermis, and a strong external ligament. The hinge carries two cardinal teeth in each valve, with a single lateral tooth posteriorly, and variably developed anterior lateral teeth (fig. 616). The genus *Cyprina* is represented in recent seas by the familiar *C. Islandica*, and there are numerous Secondary and Tertiary species, commencing in the Lias.

The genus *Isocardia* (fig. 617) comprises the "Heart-cockles," in which the shell is cordiform and inflated, and the beaks are remote and subspiral. The ligament splits in front, and is continued in two separate furrows as far as the beaks. The hinge in each valve possesses two cardinal teeth and a posterior lateral tooth. The genus *Isocardia* is represented by living forms, and the fossil species date from the Jurassic rocks. Most of the Jurassic "Heart-cockles," however, belong to the related genus *Anisocardia*, in which the beaks are approximated and the ligament is not split.

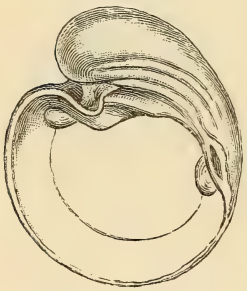


Fig. 617.—*Isocardia crassa*. Pliocene.

Cypricardia (= *Trapezium*) has a trapezoidal shell, usually radiately striated, the hinge with three radiating cardinal teeth and a posterior lateral tooth in each valve, and the posterior side often keeled. The true *Cypricardiæ* are probably wholly Mesozoic and Kainozoic, and a few recent species of the genus are known. It is possible, however, that the Palæozoic genera *Cypricardinia* (Silurian to Carboniferous) and

Goniophora (Silurian and Devonian) should find a place in the neighbourhood of *Cypricardia*.

Family 3. Veneridæ.—In this family the animal is free and locomotive; the mantle has a large anterior opening for the foot; and respiratory siphons, which may be separate or more or less united, are developed. The foot is tongue-shaped and compressed, in some cases grooved and byssiferous. The shell (fig. 618) is regular, suborbicular or oblong, equivalve, and furnished with an external ligament. The hinge usually carries three diverging cardinal teeth, and the development of the lateral teeth is variable. The pallial line usually shows a deeper or shallower sinus, but in some cases is entire. The *Veneridæ* are all marine, and the family includes some of the most highly organised and most beautifully

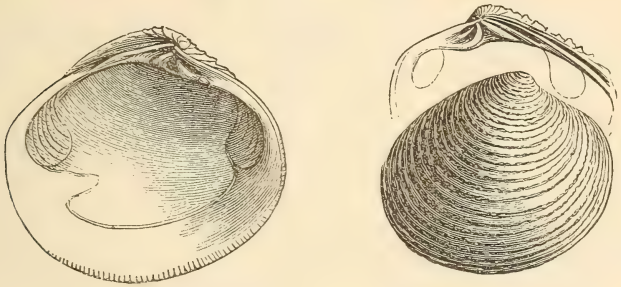


Fig. 618.—*Venus cincta*, from the Miocene rocks of Austria. (After Zittel.)

coloured examples of the entire class of the *Lamellibranchiata*. No Palæozoic representatives of the family have been as yet detected.

In the genus *Venus* (fig. 618) the shell varies greatly in form and in surface-ornamentation, and is principally distinguished by its wide hinge-plate, furnished in each valve with three diverging cardinal teeth. The genus, in its typical form, appears to begin in the Jurassic rocks, and the Tertiary rocks have yielded a large number of forms, while about two hundred species are known to exist at the present day. Very nearly related to *Venus* is the genus *Cytherea* (*Meretrix*), which is largely represented at the present day, and has numerous fossil forms, commencing in the Jurassic rocks.

In the genus *Dosinia* (*Artemis*) the shell is orbicular, compressed, and concentrically-striated, with a deep "lunule" and a deep and pointed pallial sinus (fig. 556, b). The earliest fossil forms appear in the Cretaceous rocks. *Venerupis*, again, has the shell radiately ribbed, and at the same time furnished with concentric ridges, the general form of the shell being oblong. In *Tapes*, lastly, the shell is oblong, with anteriorly placed beaks, a concentrically-striated

surface, and a broad pallial sinus. The genus is known by Cretaceous, Tertiary, and Recent species.

In the singular genus *Thetis*, now usually included here, the shell is gibbous and very thin, and there is an exceedingly deep, angular, pallial sinus, which extends nearly to the beaks. The known species of this genus are found in the Cretaceous rocks. Finally, the genus *Petricola*, now usually regarded as the type of a separate family, comprises Bivalves which differ from the *Veneridæ* in their habit of burrowing into rocks or sand, or in being fixed into crevices by a byssus. The shell in this genus is thin and tumid, with a short anterior side and a deep pallial sinus. The range of the genus is from the Cretaceous period to the present day.

Family 4. Cyrenidæ.—In this family the mantle is open in front; a single siphon is present, or, more usually, two more or less united; and the foot is large and tongue-shaped. The shell is suborbicular, closed, with a thick epidermis and a concentrically-striated surface, the hinge with cardinal and lateral teeth, and the ligament external. The pallial line is simple or slightly sinuated. The members of this family inhabit fresh or brackish waters, and their remains are commonly found in estuarine or lacustrine deposits of Mesozoic and Tertiary age.

In the genus *Cyrena* (fig. 619) the shell is thick, and rounded or subtrigonal, the beaks being commonly eroded. The hinge in each valve has three cardinal teeth, and a single lateral tooth in front and behind. The forms which are included under the name of *Corbicula* differ from *Cyrena* proper principally in the fact that the lateral teeth are elongated and are transversely striated. The oldest representatives of these two types appear in the Jurassic rocks, and there are numerous living forms, the Cretaceous and Tertiary rocks having also yielded many characteristic species.

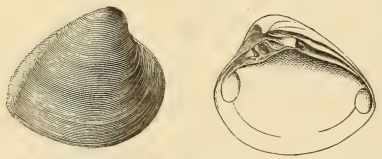


Fig 619.—*Cyrena antiqua.* Eocene.

The genus *Sphærium* (*Cyclas*) comprises fresh-water forms in which the shell is of small size, thin, more or less orbicular, and nearly equilateral. The right valve has one cardinal tooth, often bifid, and the left valve has two. The genus *Pisidium* differs from the preceding in little except that the shell is inequilateral, the anterior side being the longest. Both these types are now in existence, and the earliest fossil forms commence in the Eocene Tertiary.

Family 5. Ungulinidæ.—In this family the mantle-lobes are free; and the foot is long and vermiform, and does not secrete a byssus. The

shell is equivalve, slightly inequilateral, orbicular in form, and more or less tumid. The hinge has usually two cardinal teeth in each valve, without lateral teeth. The ligament is wholly or partially internal, and the pallial line is entire.

The type-genus of this little group is *Ungulina*, which is represented by living species and by a few Tertiary forms.

Family 6. Unicardiidæ. — In this family the shell is equivalve, slightly inequilateral, oval or rounded, and concentrically striated. The hinge carries a single cardinal tooth in each valve ; the ligament is lodged in an external marginal groove ; the adductor impressions are elliptical ; and the pallial line is entire. The genus *Unicardium* is the type of this family, and its species range from the Trias to the Chalk. Fischer also includes here his genus *Pseudedmondia*, of the Carboniferous rocks, founded for the reception of certain forms of *Edmondia* in which the ligament is external, and is placed in a marginal groove.

Family 7. Tancrediidæ.—This family includes transversely triangular shells, resembling *Donax* in form, with an external ligament, and an *entire* pallial line. The hinge has in each valve two cardinal teeth (sometimes only a single tooth in one valve), with lateral teeth as well, at any rate posteriorly. The type of this family is the extinct genus *Tancredia*, in which the shell is attenuated in front, and obliquely truncated behind. The species of this genus range from the Trias to the Chalk.

Family 8. Donacidæ.—In this family the animal is marine or estuarine in habit, with a large foot, and short separate siphons. The shell is equivalve, more or less wedge-shaped, close, and non-nacreous. The hinge carries one or two cardinal teeth in each valve, with inconstant lateral teeth ; the ligament is external ; and the pallial line is deeply indented.

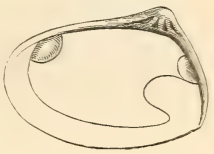


Fig. 620. — Interior of the right valve of *Donax retusa*. Eocene.

In the genus *Donax* (fig. 620), the shell is wedge-shaped, the front rounded and produced, and the posterior side short and obliquely truncated. There are numerous living species of this genus, and a small number of fossil forms, the oldest undoubted types appearing in the Eocene deposits. The Jurassic genus *Isodonta* (*Sowerbya*) may be placed in the neighbourhood of *Donax*.

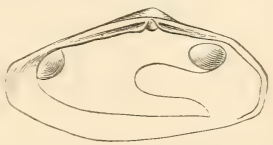


Fig. 621.—Interior of the right valve of *Psammobia rudis*. Eocene.

Family 9. Psammobiidæ.—This family includes marine Bivalves, with long separate siphons and a tongue-shaped foot. The shell is transversely elongated, equivalve, sub-equilateral, slightly gaping at both ends, with an external ligament, and a deeply sinuated pallial line (fig. 621). The hinge usually carries two cardinal teeth in each valve, but there are no lateral teeth.

The type of this family is the genus *Psammobia*, in which the

shell is oblong, compressed, and nearly equilateral (fig. 621). There are many recent species of this genus, together with a moderate number of Tertiary forms, but the earliest appearance of the genus seems to be in the Cretaceous rocks. The Jurassic genus *Quenstedtia* appears to be nearly allied to *Psammobia.*

Family 10. Solenidæ.—In this family respiratory siphons are present, and are usually short and more or less united, but may be longer and separate. The foot is very large, and more or less cylindrical in shape; and the branchiæ are prolonged into the branchial siphon. The shell is transversely elongated, more or less gaping at both ends, equivalve, and covered with epidermis. The hinge is variable, carrying from one to three cardinal teeth in each valve, without lateral teeth. The ligament is external, and the pallial line is more or less sinuated. The recent members of this family are all marine or estuarine in habit, and the group attains its maximum development at the present day.

Of the genera of this family, *Solecurtus* (fig. 622) has an elongated shell with subcentral beaks, the dorsal and ventral margins being

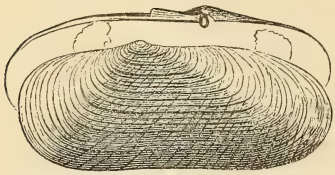


Fig. 622.—*Solecurtus Deshayesi.* Eocene. (After Zittel.)

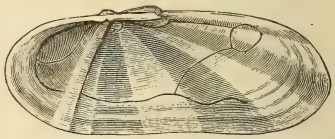


Fig. 623.—Interior of the right valve of *Siliqua polita.* Recent.

nearly parallel, and the surface generally marked with oblique lines. The genus begins in the Cretaceous rocks and still survives. In the genus *Siliqua* (fig. 623) the shell agrees in form with that of *Solecurtus*, and also has the beaks placed a little in front of the centre, but an oblique internal rib runs from below the beak to the ventral margin. This genus ranges in time, as does the preceding, from the Cretaceous to the present day. *Cultellus*, ranging from the Eocene to the present day, resembles the preceding in most characters, but the beaks are placed very far forwards, and the shell thus becomes very inequilateral. In the genera *Ensis* and *Solen* are included the typical "Razor-shells," in which the shell is greatly elongated, with the beaks placed almost at the anterior end of the shell, and with both extremities widely gaping. *Ensis* begins in the Tertiary rocks and is represented at the present day, its chief distinction from *Solen* being that the shell is somewhat curved, whereas in the latter it is straight. *Solen* itself is said to occur in deposits as old as the Devonian, but the earliest undoubted species are found in the

Trias, and the genus still survives. The Carboniferous genus *Solenopsis*, with prominent beaks and a closed anterior end, and the Devonian *Palæosolen* may represent ancient types of the *Solenidæ*. Here also, perhaps, may be placed the Palæozoic genus *Orthonota*, the typical forms of which are Devonian, though species have been described from rocks as old as the Ordovician (fig. 624). In this genus the shell is greatly elongated and very inequilateral, the anterior end being rounded and the posterior end truncate, and the beaks being close to the anterior end. The muscular impressions and pallial line have not been made out; and the hinge is only imperfectly known, but is apparently edentulous. The hinge-line is straight, and in the typical forms of the genus is continued in a straight line in front of the beaks. In one group of forms, however, sometimes distinguished under the name of *Orthodesma*, the hinge-line is bent or contracted in front of the beaks, and is straight behind (fig. 624).

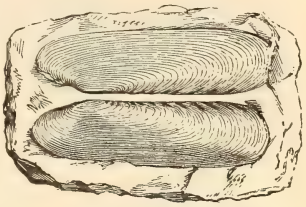


Fig. 624.—*Orthonota* (*Orthodesma*) *parallela*. Ordovician.

Order X. Myacea.

In this order the mantle-lobes are united, a pedal aperture existing in front and two siphons behind. The siphons are long, and may be united or separate. The foot may or may not be byssiferous, and there are two adductor muscles. The shell is free, equivalve or inequivalve, with an internal or external ligament, and a variable pallial line, while the characters of the hinge also differ in different families of the order. The chief families of this order are the *Mactridæ*, *Myidæ*, *Glycimeridæ*, and *Gastrochænidæ*.

Family 1. Mactridæ.—In this family the mantle is more or less open in front; the siphons are united, with fringed orifices; and the foot is compressed. The shell is equivalve, trigonal, generally gaping behind; the ligament being typically internal and lodged in a deep triangular pit between the beaks. The left valve has a widely bifurcated cardinal tooth, which is received between the diverging branches of a right cardinal tooth; and lateral teeth are usually present in addition in front and behind. The pallial line is usually deeply sinuated. The members of this family are all marine, and the two principal genera are *Mactra* and *Lutraria*.

In the genus *Mactra* (fig. 625) the shell is trigonal in form, slightly gaping behind, with a short pallial sinus. The internal ligament is contained in a triangular pit, but there is also an external ligament lodged in a groove. The recent species of

Mactra live buried in sand or mud. The fossil forms begin in the Jurassic rocks, but the genus does not show any extensive development till the Tertiary rocks are reached.

In the genus *Lutraria* the shell is oblong and gaping at both ends; the pallial sinus is deep, and the internal ligament is supported by a prominent, spoon shaped cartilage-plate. The earliest undoubted fossil forms of this genus appear in the Tertiary rocks, and about thirty living species are known.

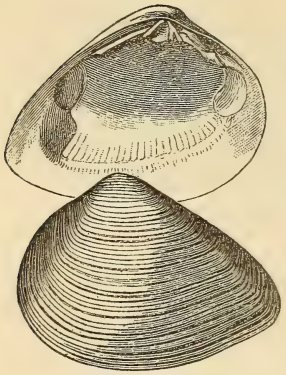


Fig. 625.—*Mactra podolica*. Miocene Tertiary, Austria. (After Zittel.)

Family 2. Myidæ.—In this family the mantle is almost entirely closed, but there exists in front an aperture for the small triangular foot, while posteriorly are two long siphons, more or less completely united with one another (fig. 555), and partly or wholly retractile. The shell is inequivalve, thick, gaping posteriorly, and not nacreous internally. The internal ligament is supported upon a spoon-shaped process developed from the hinge-plate of the left valve. The members of this family are marine or estuarine in habit, and the principal genera are *Mya*, *Corbula*, and *Neæra*.

In the genus *Mya* the shell is oblong, inequivalve, and gaping at both ends. The left valve is the smallest, and it carries an internal ligament supported upon a prominent cartilage-process (figs. 626, 627). The Myas live buried vertically in sand or mud. They are not known to have existed before the period of the Middle Tertiary (Miocene), and almost all the fossil species are in existence at the present day.

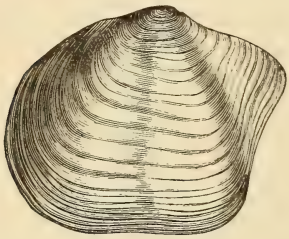


Fig. 626.—*Mya truncata*. Post-Pliocene and Recent.

Fig. 627.—Portion of the hinge of *Mya arenaria*, showing the cartilage-process.

In *Corbula* (fig. 628) the shell is inequivalve, the left valve the smallest, and with a prominent cartilage-process; but the shell is

gibbous, and does not gape at its ends, whilst the pallial sinus is small. The recent species of *Corbula* live partly in the sea, and partly in estuaries or at the mouths of rivers. There are numerous fossil forms of the genus, especially in the Cretaceous and Tertiary rocks; but the oldest forms appear in the Trias.

Fig. 628.—*Corbula pisum*, viewed from the left and right sides. Eocene.

The genus *Neæra* is allied to *Corbula*, but the shell is nearly equivalve, the right valve being slightly the smallest, and the shell is produced and open posteriorly. The earliest types of *Neæra* appear in the Upper Jurassic rocks, and the genus still survives.

Family 3. Glycimeridæ.—In this family the mantle-lobes are united, and there are long siphons, which are united wholly or in great part. The shell is equivalve or nearly so, gaping at both ends, and covered with a thick epidermis, which is prolonged over the siphons. The hinge has one or two weak cardinal teeth, or is toothless. The ligament is external, and the pallial sinus varies in depth. The Bivalves included in this family are all marine, and are either free or burrow in mud.

In *Glycimeris* (= *Panopæa*) the shell (fig. 629, A) is thick, oblong, inequilateral, and gaping at both ends. A single cardinal tooth is

Fig. 629.—A, Interior of the right valve of *Glycimeris* (*Panopæa*) *Americana*, from the Miocene rocks of North America, one-third of the natural size; B, Interior of the left valve of *Cyrtodaria* (*Glycimeris*) *siliqua*, Arctic seas, two-thirds of the natural size. (After Woodward.)

present in each valve; the pallial line is continuous, and the pallial sinus is very deep. Several Recent species of *Glycimeris* are known, and there are also various Tertiary forms, the earliest types of the genus seeming to occur in the Cretaceous rocks. Allied to the preceding is the genus *Cyrtodaria* (= the *Glycimeris* of many authors). in which the shell agrees generally with that of *Glycimeris*, but the pallial line is interrupted, and the pallial sinus is very slight (fig. 629, B).

In the genus *Saxicava* (fig. 630) the animal burrows in rocks, or fixes itself in crevices by means of a byssus. The adult shell is

thick and oblong, more or less inequivalve, irregular, and often gaping. The hinge is generally edentulous, and the pallial line is interrupted. The genus seems to commence in the Eocene Tertiary, and has continued to the present day.

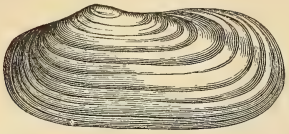


Fig. 630.—*Saxicava rugosa*, left valve. Post-Pliocene and Recent.

Family 4. Gastrochænidæ.—In this family the mantle-lobes are united; there are long siphons, joined together; and the foot is of small size, finger-shaped, and not byssiferous. The shell is equivalve, inequilateral, thin, wedge-shaped, and gaping in front. The beaks are placed anteriorly, and the anterior side of the shell is short. The hinge is toothless; the ligament is external; and the pallial sinus is deep. The members of this family burrow in rocks, corals, &c., or bury themselves in mud; and a longer or shorter shelly tube, to which the shell itself is commonly cemented, is often developed. The tubes and shells of *Gastrochæna* are not very rarely found in the fossil state in rocks of Secondary and Tertiary age, and a number of living species are known. The allied genus *Fistularia* ranges from the Cretaceous rocks to the present day.

Order XI. Adesmacea.

In this order the mantle-lobes are united, and there are long siphons joined along almost their entire length. The foot is generally well developed, and there are two adductor muscles. The shell consists essentially of two valves, but accessory plates or an adventitious calcareous tube may be developed in addition. A portion of the cardinal margin is reflected above the beaks, and the umbonal cavity is divided internally by a prominent process. The hinge and ligament are not developed. The members of this order are inhabitants of the sea or of brackish waters, and they all form perforations in stone or wood. The order is divided by Fischer into the two closely related families of the *Pholadidæ* and *Teredinidæ*.

Family 1. Pholadidæ.—In this family the animal is club-shaped or worm-like, with a short truncated foot, and long siphons united to near their extremities. The shell is gaping at both ends, with a portion of the cardinal margin reflected over the beaks, and usually having the dorsal region protected by one or more accessory plates. The members of this family are almost exclusively marine, and form burrows in stone or wood. In some cases (as in *Pholas* itself) the young are similar to the adult; whereas in other cases (*Pholadidea*, *Teredina*, &c.) a marked metamorphosis takes place in development. This metamorphosis consists essentially in the formation of a cal-

careous plate which fills up the anterior vacuity in the valves, and in the production from the hinder end of the shell of cup-shaped appendices which may coalesce to form a longer or shorter tube.

In the genus *Pholas*, the shell is cylindrical or oval, and the front portion of the valves is marked with conspicuous radiating ridges or rows of spines. The valves are edentulous; and there is no ligament, or a rudimentary one. The pallial sinus is very deep, and the dorsal margin of the shell is protected by accessory valves. The *Pholades* inhabit burrows which they form for themselves in clay, peat, or rock, and they are known in the fossil condition not only by their shells but also by their burrows, the latter affording useful indications of the existence of old shore-lines. Various extinct forms are known from the Tertiary rocks, and the genus appears to be represented in the Cretaceous and Jurassic deposits.

In the recent genus *Pholadidea* the shell has a transverse furrow, and the anterior vacuity of the valves becomes filled up with a callous plate. In the genus, or sub-genus, *Parapholas*, again, the anterior aperture becomes similarly closed by a callous plate, but the valves show two oblique furrows running from the beaks to the ventral margin (fig. 631).

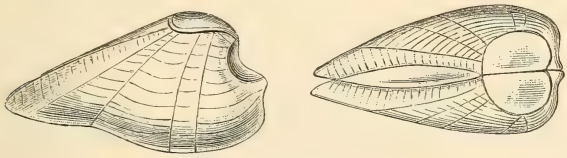


Fig. 631.—*Parapholas mersa*, viewed from one side and above. Cretaceous. (After Stoliczka.)

The species of *Parapholas* range from the Cretaceous rocks to the present day. In the allied *Martesia* the anterior vacuity is also closed by a callous plate, and the beaks are covered by a simple shield-like lamina. The living species of *Martesia* burrow in wood, and the earliest fossil forms have been detected in the Carboniferous rocks. The recent genus *Xylophaga* also comprises wood-boring forms, and is represented in rocks as ancient as the Jurassic and Cretaceous by allied types (*Xylophagella*). Lastly, Fischer places in this family the Eocene genus *Teredina*, in which there is a globular shell, the anterior vacuity of which is closed by a callous plate, while the beaks are covered by a dorsal plate, and the valves are fused with a long calcareous tube, developed posteriorly.

Family 2. Teredinidæ.—This family includes only the single genus *Teredo*, the characters of which are, therefore, those of the family. In *Teredo*, the shell is "globular, open in front and behind, lodged at the inner extremity of a burrow partly or entirely lined by shell; valves three-lobed, concentrically striated, and with one transverse furrow; hinge-margins reflected in front, marked by the anterior muscular impressions; umbonal cavity with a long curved muscular

process" (Woodward). Species of *Teredo* occasionally reach a very large size, and they are known in the fossil state both by their shells and by their burrows in wood. The genus seems to have commenced in the Lias, and is well represented at the present day. Numerous Tertiary species are known, but the recognition of the existence of the "Ship-worms" in past time very generally depends simply upon the presence of their filled-up burrows in fossil wood.

Order XII. Lucinacea.

This order includes marine Lamellibranchs, with typically but a single branchia on each side and with two adductor muscles, the mantle-lobes being more or less free, and the foot usually vermiform. The shell is free, non-nacreous, the hinge with cardinal and lateral teeth, and the pallial line entire. The only family included in this order is that of the *Lucinidæ*, the precise limits of which, as regards fossil forms more particularly, are still uncertain.

Family 1. Lucinidæ.—The mantle-lobes in this family are open below, with one or two siphonal apertures behind, and the foot is elongated, cylindrical, or strap-shaped. The shell is orbicular and free, with one or two cardinal teeth, and generally a single lateral tooth on each side. The ligament is partially or wholly internal, or

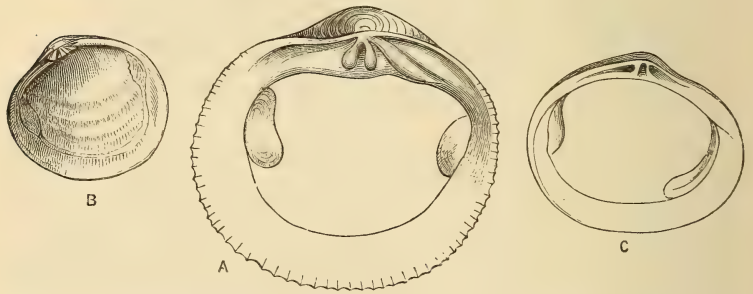


Fig. 632.—A, Interior of the right valve of *Corbis pectunculus*—Eocene; B, Interior of the right valve of *Diplodonta lupinus*—Miocene; C, Interior of the left valve of *Lucina striatula*—Jurassic.

in some cases (*Diplodonta*) external. The anterior adductor impression is usually elongated. Taken as a whole, the family is principally Secondary, Tertiary, and Recent, its Palæozoic representatives being mostly imperfectly understood, and referred here with doubt. In *Lucina* itself, the type of the family (fig. 632, C), the shell is rounded, with a lunule beneath the beak; the ligament is in a deep groove, sometimes nearly or quite internal; and the teeth have the typical arrangement of the entire group, though some are occasion-

ally obsolete. Little can be said with certainty as to the Palæozoic shells usually referred to *Lucina*, but the genus is abundantly represented in Secondary and Tertiary deposits; and ancient representatives of the genus have been described from the Silurian and Devonian rocks. *Corbis* (fig. 632, A), with many species from the Trias onwards, is very like *Lucina*, but has the surface concentrically furrowed, with denticulate edges. *Diplodonta* (Cretaceous to Recent) has two cardinal teeth in each valve, the anterior in the right and the posterior in the left being bifid (fig. 632, B). Lastly, the genus *Axinus* of Sowerby may perhaps be referred here, though the hinge is toothless or has only a feeble tooth in the right valve. The range of this genus is from the Eocene to the present day.

Order XIII. Tellinacea.

In this order the foot is very large; there are two adductor muscles; there is only a single gill on each side; and the siphons are long and completely separate. The shell is free, non-nacreous, the hinge with cardinal and lateral teeth, and the pallial line deeply sinuated. This order includes the two families of the *Tellinidæ* and *Scrobiculariidæ*, all the members of which are marine in habit.

Family 1. Tellinidæ.—In this family the shell is free, usually equivalve and closed, with smooth margins. The hinge has at most two cardinal teeth in each valve, with a lateral tooth on each side, or without lateral teeth. The ligament is external, and the pallial sinus is very deep.

The principal genus in this family is *Tellina* itself, which includes about three hundred living species and a considerable number of fossil forms, mostly from the Tertiary rocks. In this genus the shell is oval or transversely elongated, very slightly inequivalve, the anterior side being rounded, and the posterior side often angulated. The beaks are often placed nearly in the middle of the shell; the ligament is prominent and external; and the pallial sinus is very broad and deep. The oldest undoubted forms of *Tellina* appear in the Lower Cretaceous rocks.

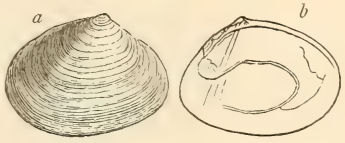


Fig. 633.—*Tellina proxima*, right valve. Post-Pliocene.

Family 2. Scrobiculariidæ.—In this family the animal agrees with that of *Tellina* in general structure, and the characters of the shell are in most respects the same; but the ligament is internal, and is lodged in a pit below the beaks, an external ligament being sometimes imperfectly developed as well. The two principal genera

are *Scrobicularia* and *Semele*, both of which are represented by Tertiary and Recent species.

Order XIV. Anatinacea.

This order includes marine Bivalves with a moderate-sized, grooved, or byssiferous foot, distinct siphonal orifices, a single branchia on each side, and two adductor muscles. The shell is thin, usually with a pearly internal layer and a finely granulated external layer. The hinge may or may not carry teeth, and the pallial line is mostly sinuated, but may be entire. The principal families included in this order are the *Solemyidæ*, *Arcomyidæ*, *Anatinidæ*, *Grammysiidæ*, *Præcardiidæ*, *Pholadomyidæ*, and *Clavagellidæ*.

Family 1. Solemyidæ.—This family includes the single genus *Solemya*, which ranges from the Devonian to the present day. In this genus the shell is equivalve, inequilateral, transversely elongated, obtuse and gaping at both ends, with the epidermis prolonged beyond the ventral margin. The beaks are inconspicuous; the ligament is partly internal and partly external; the hinge is toothless, or has a single cardinal tooth in each valve; and the pallial line is obscure. The Devonian and Carboniferous genus *Clinopistha* appears to be related to *Solemya*.

Family 2. Arcomyidæ.—The forms included in this family are all extinct, and have usually been included in the *Pholadomyidæ*, from which they are distinguished by the finely granulated character of the exterior of the shell. The shell is equivalve, inequilateral,

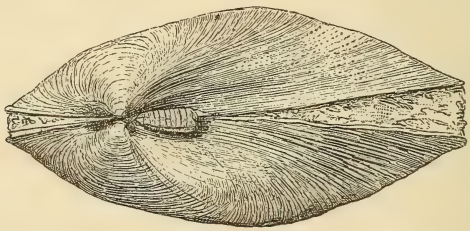


Fig. 634.—*Arcomya* (*Homomya*) *calceiformis*, viewed from the dorsal side, two-thirds of the natural size. Lower Jurassic rocks. (After Zittel.)

very thin, with an edentulous hinge, but with a thickened cardinal margin. The ligament is external and prominent, and the pallial line is sinuated. The principal genera included in this family are *Arcomya* (fig. 634), *Goniomya*, and *Pleuromya*, all of which are confined to the Secondary rocks, the first and last ranging from the Trias to the Chalk, while *Goniomya* is Jurassic and Cretaceous.

Family 3. Anatinidæ.—In this family the mantle-lobes are more

or less united; there are long siphons, more or less extensively conjoined, and the foot is of small size. The shell is thin, usually nacreous internally, and commonly granulated externally, and as a rule somewhat inequivalve. The ligament is wholly or partially internal, usually in a spoon-shaped cartilage-pit, flanked by one or two cardinal teeth, and often containing a detached ossicle. The pallial line is usually sinuated. All the members of this family are inhabitants of the sea.

In *Anatina* itself (fig. 635) the shell is oblong, very thin, gaping behind, and having the beaks turned towards the posterior side of the shell, which is more or less attenuated. The hinge of each valve carries a spoon-shaped cartilage-process, and the beak is usually supported by an oblique, backwardly directed internal ridge. The pallial line is deeply sinuated. The earliest undoubted forms of *Anatina* are found in the Lower Cretaceous rocks, and the genus survives at the present day. The genus *Thracia*, ranging from the Trias to the present day, is in most respects very similar to *Anatina*, but the shell is inequivalve (the right valve being larger than the left), and there is a short external ligament, in addition to the internal cartilage. In *Pandora* the shell is also thin and inequivalve, but it does not gape behind. The species of this genus range from the Eocene to the present day; and the species of the allied genus *Lyonsia* have a similar range in time. Lastly, the Cretaceous genus *Liopistha* appears to belong here, though the pallial line is apparently not sinuated. Numerous Palæozoic Bivalves have been referred to the *Anatinidæ*, but most of these are characterised by an entire pallial line and an external ligament, and may be provisionally placed in the family of the *Grammysiidæ*. It is possible, however, that the genus *Allorisma* (fig. 636, c) should find a place in the *Anatinidæ*, with which it agrees in the possession of a sinuated pallial line, and in having the external surface of the valves granulated. The shell in this genus is transversely elongated, equivalve, with anteriorly-placed, almost terminal beaks, and a concentrically-striated surface. The hinge is edentulous, and an external ligament is present. The species of *Allorisma* range from the Devonian to the Permian rocks.

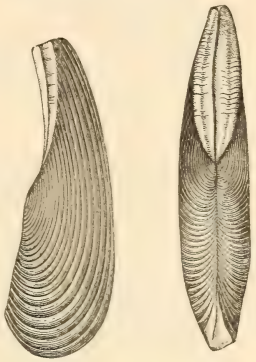


Fig. 635.—*Anatina spatulata.*
Kimeridge Clay (Upper Oolites.)

Family 4. Grammysiidæ.—This family comprises a number of Palæozoic Bivalves which differ from the typical *Anatinidæ* in having an entire pallial line, and also in the fact that the ligament is

external. The shell in the forms included here is equivalve, oval or transversely elongated, convex, and thin. The hinge is edentulous, and the cardinal border is straight. Fischer regards this family as representing in the Palæozoic deposits the *Arcomyidæ* of the Secondary period, but the affinities of most of the genera provisionally associated with *Grammysia* must be regarded as very uncertain.

In the Silurian and Devonian genus *Grammysia* (fig. 636, B) the shell is transversely elongated, equivalve, with the beaks placed very

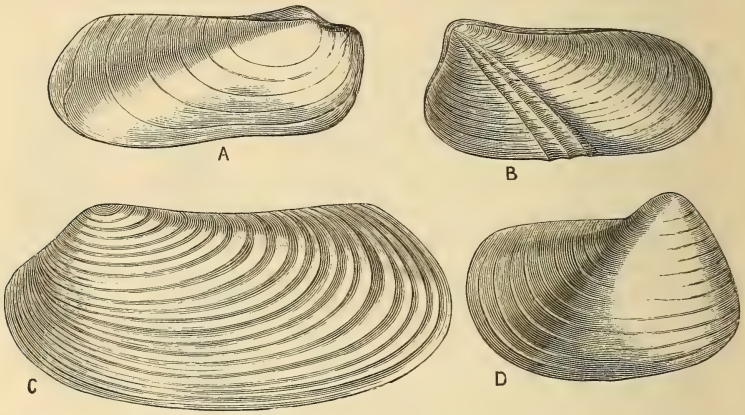


Fig. 636.—A, Right side of *Palæanatina typa*, showing the superior size of the left beak—Devonian (after Hall); B, *Grammysia cingulata*—Silurian; C, *Allorisma sulcata*—Carboniferous (after Phillips); D, *Leptodomus truncatus*—Silurian (after M'Coy).

far forwards and incurved, a deep "lunule" being present below them. The hinge-line is straight, and the hinge is edentulous; and a single or double fold extends backwards from the beaks to the middle of the ventral margin.

The following Palæozoic genera agree with *Grammysia* in more or fewer characters, and may be provisionally associated with it, though they diverge in important respects from the above general definition of the family *Grammysiidæ*. In *Cardiomorpha* (Silurian to Carboniferous) the shell is shaped like that of *Isocardia*, with approximated, almost terminal beaks, and a simple pallial line. The hinge is toothless, and there is an elongated groove for the external ligament. In the genus *Leptodomus*, with a similar geological range to the preceding, the shell (fig. 636, D) is thin and elongated, with tumid incurved beaks, a well-marked posterior slope, and a deep "lunule." The hinge is toothless, and the surface is marked with concentric ridges which split anteriorly. The widely distributed Carboniferous genus *Edmondia* has "a transversely-oval, equivalve, edentulous shell, with an internal lamellar cartilage-support. The dorsal margins are erect and simple, and the pallial line is entire" (R. Etheridge, jun.) In the genus *Sanguinolites*, principally if not exclusively Carboniferous in its range, the shell is "transversely oblong and

equivalve, but very inequilateral, possessing an external ligament, and a strong external oblique posterior ridge, the pallial line being entire" (R. Etheridge, jun.) The Carboniferous genus *Anthracomya*, in which there is a thin concentrically-striated oblong shell, with anterior beaks and an external ligament, may perhaps also find a place here. The Devonian genus *Palæanatina* (fig. 636, A) more probably belongs to the *Anatinidæ*, since the shell is inequivalve (the left valve being larger than the right), and there are indications of the presence of an internal ligament; but the form of the pallial line has not been clearly ascertained. The Devonian genus *Cimitaria* also occupies an uncertain position; and there are various other Palæozoic types which may possibly be referable to this family, but which cannot be discussed here.

Family 5. Præcardiidæ.—This family has been constituted by Hoernes for the reception of a number of Silurian Bivalves, of which the genus *Præcardium* is the type. The forms here in question have thin equivalve or inequivalve shells, which have a marked general resemblance to the Cockles, but which are without the characteristic teeth of the *Cardiidæ* — the hinge being, in fact, edentulous, or furnished with transverse folds. The adductor impressions and pallial line in *Præcardium* and its allies are unknown; but Fischer suggests that the genus *Cardiola* may possibly be found to belong to this singular group.

Family 6. Pholadomyidæ.—In this family the mantle-lobes are united; and there are very long siphons, conjoined along their entire length. The foot is small, and a single gill is present on each side. The shell is equivalve, inequilateral, thin, convex, adorned with radiating ribs, pearly internally, but not granulated externally. The hinge is toothless; the ligament is external; and the pallial line is sinuated. This family has close relationships with the *Arcomyidæ* and also with the *Anatinidæ*, and the only genus included in it by Fischer is *Pholadomya* itself, which is extremely abundant in the Jurassic, Cretaceous, and Tertiary rocks, but is only known at the present day to be represented by two or three species, all of which inhabit great depths in the sea.

In *Pholadomya* (fig. 637) the shell is equivalve, oblong, and gaping posteriorly, thin, ventricose, and adorned with radiating ribs on the sides. The anterior side of the shell is short and rounded, and the beaks are prominent. The hinge is toothless, and the cardinal margin behind the beaks is often folded in so as to give rise to an elongated false area or escutcheon.

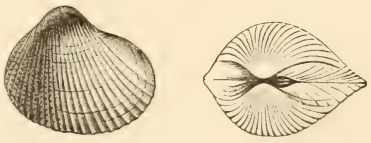


Fig. 637.—*Pholadomya æquivalvis.* Chalk.

Family 7. Clavagellidæ.—In this family the mantle-lobes are

united, and there are long conjoined siphons, with a single branchia on each side. The shell is in the young state similar to that of *Thracia*, but one or both of the valves ultimately become fused with a secondarily-produced adventitious calcareous tube, of considerable size (fig. 638).

The genus *Clavagella* itself comprises forms which burrow in rocks, corals, &c., and in which the shell is inequivalve, the left valve being fused with a long calcareous tube (fig. 638), while the right valve lies freely in the interior of the tube, the latter being often divided by a longitudinal partition. This singular genus is known to have existed in rocks as old as the Cretaceous, and still survives. In the nearly allied genus *Aspergillum* (Pliocene and Recent), both the valves of the shell are fused with the calcareous tube, which is closed below by a perforated disc with a minute central fissure.

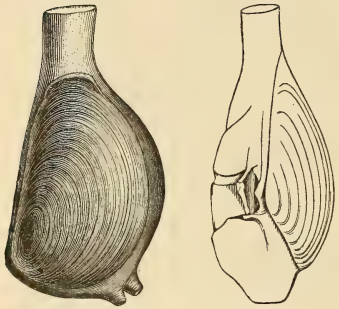


Fig. 638.—*Clavagella cretacea.* Chalk.

CHAPTER XXXVII.

Class II. Gastropoda (or Gasteropoda).

The members of this class are *Mollusca with a more or less distinct head, and a generally unsymmetrical body. The mantle is never divided into two lobes, and the shell, when present, is univalve. The "foot" is well developed, and usually has the form of a broad horizontally-flattened ventral disc, upon which the animal creeps.*

The body in the Gastropods is composed of three principal portions—a head, foot, and visceral sac—the last of these being more or less completely protected by a fold of the dorsal integument, constituting the "mantle." The body is distinctly unsymmetrical, and the mantle is never divided into a right and left lobe, while the visceral sac is often coiled up spirally. The foot is typically in the form of a broad flattened muscular disc, developed upon the ventral surface of the body, and not exhibiting any distinct division into parts. In the *Heteropoda*, however, and in the Wing-shells (*Strombidæ*), the foot exhibits a division into three portions: an anterior, the "propodium"; a middle, the "mesopodium"; and a posterior lobe, or "metapodium." In the *Heteropoda*, the foot is flattened, and forms a ventral fin, by means of which the animal swims, back-downwards.

In some, again, the upper and lateral surfaces of the foot are expanded into muscular side-lobes, which are called "epipodia." In the Pteropodous division of the Gastropods the epipodia are the only portions of the foot which are developed, and they constitute a pair of fins attached to the sides of the head. In many cases the metapodium, or posterior portion of the foot, secretes a calcareous, horny, or fibrous plate, which is called the "operculum" (fig. 639, *o*), and which serves to close the orifice of the shell when the animal is retracted within it.

The *shell* of the Gastropods is a secretion from the mantle, and is always present in the embryo. It is, however, wanting in the adults of the Nudibranchs and in some other forms, and it is in other

cases very minute, and hidden in the mantle (as, for example, in the Slugs). From the very general occurrence of a shell which is "univalve," or composed of a single piece, the Gastropods are commonly spoken of as the "Univalve Molluscs." In its chemical composition the shell is composed of carbonate of lime (sometimes in the condition of calcite, sometimes in that of aragonite). Its inner layer is often nacreous, and it grows by additions made to its free margin by the muscular edge ("collar") of the mantle, in which

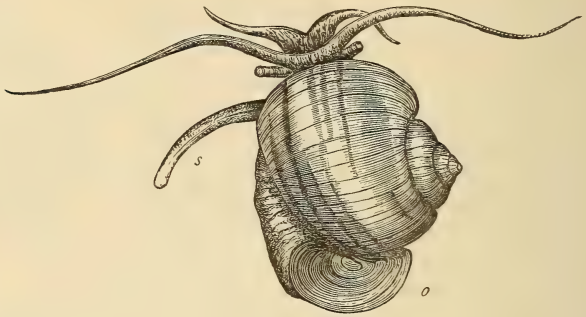


Fig. 639.—*Ampullaria canaliculata.* *o*, Operculum; *s*, Respiratory siphon.

numerous pigment-glands are contained. Primitively the shell is covered with a horny cuticular layer ("epidermis"), but this often disappears with age. In many cases, the mantle becomes reflected over the shell, the outer surface of which may thus become covered with a layer of enamel (as in the Cowries).

The shell of the Gastropods is to be regarded as essentially a cone, the apex of which is more or less oblique. In the simplest form of the shell, the conical shape is retained without any alteration, as is seen in the common Limpet (*Patella*). In the great majority of cases, however, the cone is considerably elongated, so as to form a tube, which is usually coiled up into a spiral. The "spiral univalve" (fig. 640) may, in fact, be looked upon as the typical form of the shell in the *Gastropoda*. In some cases the coils of the shell—termed technically the "whorls"—are hardly in contact with one another (as in *Vermetus*). More commonly the whorls are in contact, and are so amalgamated that the inner side of each convolution is formed by the pre-existing whorl. In some cases the whorls of the shell are coiled round a central axis *in the same plane*, when the shell is said to be "discoidal" (as in the common fresh-water shell *Planorbis*). In most cases, however, the whorls are wound round an axis in an oblique manner, a true spiral being formed, and the shell becoming "turreted," "tro-

choid," "turbinated," &c. This last form is the one which may be looked upon as most characteristic of the Gastropods, the shell being composed of a number of whorls (fig. 640, *wh*) passing obliquely round a central axis or "columella" (*co*), having the embryonic shell or "nucleus" at its apex (*a*), and having the mouth or "aperture" of the shell placed at the extremity of the last and largest of the whorls, termed the "body-whorl" (*wh'*). The lines or grooves formed by the junction of the whorls are termed the "sutures" (*su*), and the whorls above the body-whorl constitute the "spire" (s) of the shell. The axis of the shell (columella), round which the whorls are coiled, is usually solid, when the shell is said to be "imperforate"; but it is sometimes hollow, when the shell is said to be "perforated," and the aperture of the axis near the mouth of the shell is called the "umbilicus." The margin of the "aperture" of the shell is termed the "peristome," or "peritreme," and is composed of an outer and inner lip, of which the former (fig. 640, L) is often expanded or fringed with spines. When these expansions or fringes are periodically formed, the place of the mouth of the shell at different stages of its growth is marked by ridges or rows of spines, which cross the whorls, and are called "varices." In certain groups of the Gastropods (*Holostomata*) the aperture of the shell is unbrokenly round or "entire," but in other groups (*Siphonostomata*) it is notched, or produced into a canal. Often there are two of these canals, an anterior and a posterior, and the function of these is to protect the respiratory siphons. The animal withdraws into its shell by a retractor muscle, which passes into the foot, or is attached to the operculum; its scar or impression being placed, in the spiral Univalves, upon the columella. In the great majority of the Univalves the shell is coiled to the left, the "mouth" of the shell being thus on the right-hand side (fig. 640). In such cases the shell is said to be right-handed or "dextral." In other cases, however, the shell is coiled to the right, and the mouth

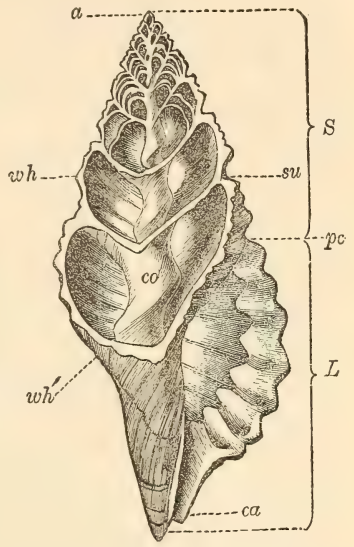


Fig. 640.—Longitudinal section of *Triton corrugatum*. S, Spire; L, Outer lip of the aperture of the shell; *a*, Apex; *wh*, The last whorl of the spire; *wh'*, The body-whorl; *su*, Suture; *ca*, Anterior canal; *pc*, Posterior canal.

is on the left, when the shell becomes "reversed" or "sinistral." The left-handed spiral may be the normal condition of the shell, or it may be only a variety of a normally dextral form.

As regards their internal anatomy, the head of the Gastropods is usually very distinctly marked out, and is generally provided with tentacles and eyes. Within the pharynx is found the singular dental apparatus which is known as the "odontophore." The essential portion of this is a chitinous band, which is beset with minute transversely-arranged teeth, and is known as the "radula" or "lingual ribbon." The radula is supported upon a cartilaginous cushion, which can be made to rotate by special muscles, the ribbon thus coming to act as a file, rasp, or chain-saw. The arrangement of the teeth in the radula varies much in different cases, but they are usually disposed in a median series, flanked by two or more lateral rows; and their form and disposition are so constant as to afford one of the most valuable aids to the classification of the recent *Gastropoda*. As, however, the characters of the radula cannot be determined in the case of fossil Gastropods, a classification based upon the structure of this organ is necessarily defective from a palæontological point of view.

Respiration in the Gastropods is variously effected; the members of one great section (*Branchiogastropoda*) being, with few exceptions, constructed to breathe air dissolved in water, while in another division (*Pulmogastropoda*) the respiration is aerial. In the former division, respiration may be effected in several ways. Firstly, there may be no specialised respiratory organ, the blood being simply exposed to the water in the thin walls of the mantle-cavity (as in some of the *Heteropoda*). Secondly, the respiratory organs may be in the form of outward processes of the integument, exposed in tufts on the back and sides of the animal (as in the *Nudibranchiata*). Thirdly, the respiratory organs are in the form of pectinated or plume-like branchiæ, contained in a more or less complete branchial chamber formed by an inflection of the mantle. In many members of this last section the water obtains access to the gills by means of a tubular prolongation or folding of the mantle, forming a "siphon" (fig. 639, *s*), the effete water being expelled by another posterior siphon similarly constructed. The number of gill-plumes differs in different groups. In most cases there is only a single branchial plume, placed on the right side of the neck; in other cases an additional gill is present on the left side; and in other forms, again (*e.g.*, *Patella*), the gills are multiple and are arranged in a circle. Lastly, in the Pulmonate Gastropods the breathing-organ is a pulmonary chamber, formed by an inflection of the mantle, the walls of which are richly supplied with blood, while air is admitted to its interior by a distinct aperture. A tran-

sition between the Branchiate and Pulmonate groups is effected by forms like *Ampullaria*, in which gills are present, but the walls of the mantle-cavity are in parts highly vascular, and are thus adapted for aerial respiration. Another link between these two groups is afforded by forms like the *Cyclostomidæ* and the *Helicinidæ*, in which the general organisation of the animal is that of the Prosobranchiate Gastropods, but the breathing-organ is a pulmonary chamber.

A few Gastropods retain the eggs within the uterus until they are hatched; but the majority are oviparous. The eggs are often laid in the form of a string or band ("nidamental ribbon"); or they may be enclosed in horny capsules (as, for example, in the common Whelk). The young, when first hatched, are provided with an embryonic shell, which in the adult may become concealed in a fold in the mantle, or may be entirely lost. In the common spiral Univalves the embryonic shell remains at the summit of the spire, as the "nucleus" of the adult shell. In the branchiate Gastropods the embryo is protected by a small nautiloid shell, and passes through a "veliger" stage, swimming freely by means of a ciliated, often lobed "velum." Among the Pulmonate Gastropods, those which are strictly terrestrial pass through no metamorphosis, the "velum" being absent in the embryo.

As regards their *classification*, the Gastropods may be divided into the two primary groups, or sub-classes, of the *Branchiogastropoda* and the *Pulmogastropoda*, the *general* distinction between the two divisions being that the animal in the former is adapted for an aquatic mode of respiration, while in the latter the breathing-organ is a pulmonary sac. The division of the Branchiate Gastropods may, again, be divided into the four orders of the *Prosobranchiata* (the ordinary Univalves), the *Opisthobranchiata* (the Sea-slugs), the *Pteropoda* (the Winged Snails), and the *Heteropoda;* while the Pulmonate Gastropods may be divided into the two orders of the *Stylommatophora* and *Basommatophora*, in accordance with the position of the eyes. The Chitons (*Polyplacophora*) and the *Dentaliidæ* (*Scaphopoda*), often included among the *Gastropoda*, will be here regarded as constituting two separate classes of *Mollusca*.

As regards their *distribution in space*, the Heteropods, the Pteropods, the Opisthobranchiates, and the great majority of the Prosobranchiates are inhabitants of the sea. Certain groups of the Prosobranchiates, however, are found either in brackish or in fresh waters; while the terrestrial groups of the *Cyclostomidæ*, *Aciculidæ*, and *Helicinidæ*, often placed among the Pulmonate Gastropods, are now usually regarded as being essentially Prosobranchiates modified for an aerial mode of respiration. The Pteropods and the Heteropods

are oceanic in habit, and are found swimming in the open sea, near the surface, far from land; but the majority of the marine Prosobranchs and the Opisthobranchs are inhabitants of shallow seas, or live between tide-marks. In depths beyond five hundred fathoms the number of Gastropods is greatly reduced; but a few forms are found to inhabit depths of between two and three thousand fathoms, or even more. The Pulmonate Molluscs, lastly, are exclusively terrestrial in habit, or live in fresh waters. In the latter case, the animal either comes to the surface from time to time, for the purpose of obtaining air, or, if the water be too deep to allow of this, its pulmonary chamber is so far modified that it is enabled to breathe the oxygen dissolved in the surrounding water.

As regards their *distribution in time*, the Branchiate Gastropods are necessarily more largely represented as fossils than the Pulmonate forms. The record of the Prosobranchiates, owing to their possession of a calcareous shell and their aquatic habits, is a very full one. On the other hand, the Opisthobranchiates are but imperfectly represented in past time, the entire group of the Nudibranchs being unprovided with a shell, and being therefore unknown in the fossil condition. The oceanic group of the Heteropods (if the *Bellerophontidæ* be placed elsewhere) is only represented in the latest Tertiary deposits; while the Pteropods, also pelagic in habit, occur as fossils in the older Palæozoic rocks, but are singularly absent from the greater part of the Mesozoic and Kainozoic formations. Of the Pulmonate Gastropods, those forms which live habitually in fresh water (*e.g.*, the *Limnæidæ*) are naturally more largely represented in the fossil condition than the purely terrestrial forms (*e.g.*, the *Helicidæ*); but the remains of the latter are not uncommon in deposits which have been formed under suitable conditions.

The Gastropods appear for the first time in the Upper Cambrian deposits, from which a number of forms have been obtained, all belonging to the holostomatous division of the Prosobranchiates, the two principal genera being *Murchisonia* and *Pleurotomaria*. The Upper Cambrian rocks have also yielded the oldest examples of *Hyolithes* and its allies, which are usually regarded as belonging to the *Pteropoda*. In the Ordovician and Silurian rocks are found very numerous types of the Prosobranchiate Gastropods, all of which—with the apparent exception of such forms as *Subulites* and *Euchrysalis*—are holostomatous. The predominant groups in these ancient deposits are the *Euomphalidæ*, *Pleurotomariidæ*, and *Bellerophontidæ*. The Pteropods are represented by the aberrant types *Conularia*, *Hyolithes*, and *Tentaculites*. In the Devonian, Carboniferous, and Permian formations the general character of the Gastropodous fauna undergoes little change, the predominating

forms still belonging to the holostomatous Prosobranchiates and the Pteropods. The latter, however, are now in part represented by such normal forms as *Styliola*. In the Carboniferous rocks, further, appear the first representatives of the Pulmonate Gastropods (*Zonites*, *Physa*, &c.)

In the Trias the Gastropodous fauna has, in the main, a Palæozoic facies, but unquestionable siphonostomatous Prosobranchiates appear here (*Cerithium*, *Purpurina*, &c.) The peculiar Palæozoic Pteropods (with the exception of *Conularia*) have now disappeared. In the Jurassic rocks a further change occurs, and a marked development of the siphonostomatous Prosobranchiates now takes place. The first Opisthobranchs appear at this stage, and we meet here with a number of existing genera of fresh-water Gastropods (*Planorbis*, *Paludina*, *Melania*, &c.) In the Cretaceous rocks the siphonostomatous Prosobranchiates continue to increase in number, and in the Tertiary period they become the predominant group, the Gastropods as a whole becoming at the same time the predominant group of the *Mollusca*, a condition of things which still subsists at the present day.

CHAPTER XXXVIII.

DIVISIONS OF THE GASTROPODA.

Sub-Class I. Branchiogastropoda.

This primary division of the Gastropods is distinguished, speaking generally, by the fact that the animals included in it are water-breathers, respiration being effected by the thin walls of the mantle-cavity, by external branchial tufts, or by pectinated or plume-like gills contained in a more or less complete branchial chamber. The groups of the *Cyclostomidæ*, *Aciculidæ*, and *Helicinidæ*, from the general characters of their organisation, must, however, be placed in this division; although the animal in these is terrestrial, and is furnished with a pulmonary chamber adapted for breathing air directly.

This sub-class comprises the four orders of the *Prosobranchiata*, *Opisthobranchiata*, *Pteropoda*, and *Heteropoda*.

Order I. Prosobranchiata.

The great majority of the members of this order are aquatic in habit, and possess gills situated in front of the heart, the auricle of the heart being thus placed in front of the ventricle. The *Cyclostomidæ*, *Aciculidæ*, and *Helicinidæ* alone possess a pulmonary chamber. The gills are, typically, plume-like, and are lodged in a branchial chamber formed by a fold of the mantle, which may or may not be so disposed as to form an anterior and posterior tube or "siphon," for the entrance and escape of water from the branchial chamber. The foot in the Prosobranchiates is large and adapted for creeping, and the sexes are distinct. Those members of the order which possess an anterior siphon for the admission of water to the branchial cavity, have the mouth of the shell notched in front, or produced into a canal in which the siphon is lodged (fig. 642); while a similar notch or canal may exist at the posterior end of the shell-aperture (fig. 643). The shell in these forms is said to be "siphonostomatous."

In a great many forms, on the other hand, siphons are not developed, and the mouth of the shell is simply rounded or "entire" (fig. 641), when the shell is said to be "holostomatous."

The great majority of the *Prosobranchiata* are inhabitants of the sea, but certain groups are restricted to fresh or brackish waters; while the *Cyclostomidæ*, *Aciculidæ*, and *Helicinidæ* are terrestrial in habit. As regards their distribution in time, the palæontological record is fuller in the case of the Prosobranchiates than it is in the case of any other division of the Gastropods. The Palæozoic types of the Prosobranchiates belong almost exclusively to forms in which the shell is "holostomatous." On the other hand, forms with the "siphonostomatous" type of shell-mouth do not make an undoubted

Fig. 641.—*Scalaria Grænlandica*, a holostomatous Univalve.

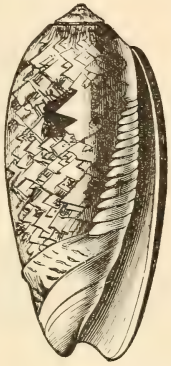


Fig. 642.—*Oliva porphyria*, a siphonostomatous Univalve.

Fig. 643.—*Cerithium aluco*, showing an anterior and posterior notch for the siphons.

appearance till the Trias is reached, and they become the predominant group of Prosobranchiates in the Tertiary rocks, which position they still hold.

The possession of a "holostomatous" or "siphonostomatous" shell has been employed as the basis for a separation of the *Prosobranchiata* into two primary sections—viz., the *Holostomata* and *Siphonostomata*—but these names, though convenient as general terms, do not indicate natural divisions. In the more modern and more scientific classification now generally in use among Malacologists the characters of the "radula" or lingual ribbon are those mainly relied upon as distinguishing the primary groups of Prosobranchiates. The form of the "radula" is, however, necessarily unknown in the case of fossil forms, and it is therefore only by means of analogies—which may or may not be trustworthy—that the extinct groups of Prosobranchiates can be ranged in a series

the groups of which are based upon the structure of this organ. All that will be attempted here, therefore, is to give a brief outline of the characters and geological range of the principal families of Prosobranchiates, without regard to the arrangement of these in larger groups. In this outline the "holostomatous" families, as the most ancient and the least highly organised, naturally take precedence of the forms with a "siphonostomatous" shell.

Family 1. Patellidæ.—In this family the animal usually possesses a series of branchiæ arranged marginally in a more or less complete cycle round the foot. The shell is conical, with the apex turned more or less clearly towards the front; and the muscular impression is horse-shoe-shaped and open in front, continuous or broken up into separate cavities. The genus *Acmæa*, often regarded as the type of a special family, differs from *Patella* proper in the fact that there is always a cervical branchial plume, the marginal gills being sometimes present, sometimes absent. As these types, however, cannot be distinguished from one another by their shells alone, this distinction is palæontologically inapplicable.

The typical species of *Patella*, such as the common Limpet (*P. vulgata*), have usually a radially-ribbed shell, with the apex subcentral and turned forwards. Such types are clearly recognisable in the Cretaceous and Tertiary rocks. In *Helcion*, again, the shell is radially-ribbed, and the apex is shifted far forwards. Such types abound in the Jurassic and Cretaceous rocks, and still survive. In *Acmæa*, finally, the apex is usually subcentral and the surface is

Fig. 644.—*Tryblidium* (*Metoptoma*) *Nycteis*, from the Ordovician of Canada. *a*, Side view; *b*, View of the upper side. (After Billings.)

generally smooth or feebly striated. This type cannot be clearly separated from the preceding except by an examination of the animal, but many of the fossil Limpets doubtless belong here. A Limpet of this type has been described by Hall from the Upper Cambrian (Potsdam Sandstone) of North America under the generic name of *Palæacmæa*.

Most of the Palæozoic Limpets belong to the genera *Tryblidium* and *Metoptoma*, which agree with one another in the fact that the shell (fig. 644) is in the form of an obtuse or shallow cone, with the apex placed very far forwards, so as to be submarginal. In *Tryblidium*, as shown by

Lindström, the muscular scar is in the form of six pairs of disconnected impressions, arranged in an oblong circle which is open in front. The species of this genus are principally Ordovician and Silurian. *Metoptoma*, as now restricted, differs from the preceding in having the anterior side broadly truncated (fig. 645, F), and in the fact that the muscular scar is in the form of a continuous horse-shoe. The genus appears to range from the Ordovician to the Carboniferous, but as the interior markings of many species are unknown, it is impossible at present to sharply separate this type from *Tryblidium*.

Family 2. Fissurellidæ.—In this family the animal has the gills symmetrically disposed on the two sides of the body. The shell is conical and limpet-shaped, with a notch in the anterior

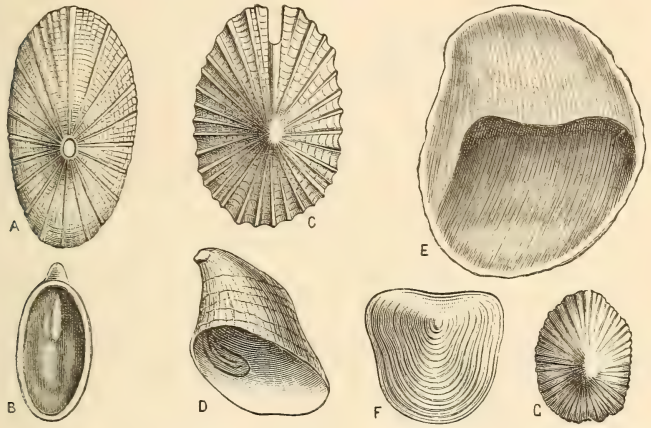


Fig. 645.—Fissurellidæ, Capulidæ, and Patellidæ. A, *Fissurella labiata*—Eocene; B, *Rimula Blainvillei*—Eocene; C, *Emarginula Guerangeri*—Cretaceous; D, *Hipponyx cornucopiæ*—Eocene; E, *Crepidula costata*—Miocene; F, *Metoptoma imbricata*—Carboniferous; G, *Patella costaria*—Eocene.

margin, or a perforation at or near the apex, corresponding with the anus (fig. 645, A and C). The muscular impression is horse-shoe-shaped and is open in front.

The genus *Fissurella* (fig. 645, A) comprises the so-called "Key-hole Limpets," distinguished by having the apex of the shell perforated by a larger or smaller, generally oval aperture. Very dubious examples of the genus have been described from the Devonian and Carboniferous rocks, but the earliest undoubted types appear in the Jurassic rocks, from which time the genus has continued to the present day. In the genus *Rimula* (fig. 645, B), ranging from the Lias to the present day, the perforation, instead of being at the apex of the shell, is placed a little above the anterior margin. Lastly, in *Emarginula* (fig. 645, C) the anterior margin is furnished with a longitudinal notch or slit. The oldest species of this genus has

been found in the Carboniferous Limestone, but most of the fossil forms are Cretaceous and Tertiary.

Family 3. Capulidæ (=*Calyptræidæ*).—In this family the shell is conical and patelliform, with a more or less spiral apex, the interior being simple, or divided by a shelly process to which the adductor muscle is attached. The margin of the shell-aperture is thin and entire, often more or less modified in outline by the habit which the animal possesses of fixing itself, with the aperture closely fitted, to some foreign body, such as a Crinoid.

The genus *Calyptræa*, in the wide sense in which it has generally been defined, includes the so-called "Cup-and-saucer Limpets," in which the interior has a half-cup-shaped process attached to the apex of the shell, and open in front. The earliest forms of this type appear in the Cretaceous rocks, and the genus still survives. In the genus *Crepidula* (fig. 645, E) there is a shelly partition covering the posterior half of the interior of the shell. The fossil forms of this genus date from the Cretaceous period. *Hipponyx*, again, comprises thick and obliquely conical shells, with a posterior apex, and often provided with a shelly basis marked by a distinct horse-shoe-shaped muscular impression (fig. 645, D). The genus ranges from the Cretaceous rocks to the present day.

By far the most important genus of this family, palæontologically speaking, is *Capulus* (*Pileopsis*) itself, including the so-called "Bonnet-limpets" of the present day. The Palæozoic shells which have been included under the name of *Platyceras* (=*Acroculia*) appear to be identical with *Capulus*, or, at any rate, to be distinguished from this by characters of no more than sub-generic value. In the genus *Capulus*, employing this name in the general sense indicated above, the shell is conical, with a posterior sub-spiral apex, and, generally, a horse-shoe-shaped muscular impression. The aperture is greatly enlarged, and its margins are essentially entire; but owing to the fact that the shell is usually affixed for lengthened periods to foreign bodies, the lips may become more or less sinuated or undulated (figs. 646, 647). The shells of this genus may, as a rule, be recognised by their obliquely-spiral or straight, conical shape, their wide aperture, and the absence of a columella. They may be dextral or sinistral, and the surface may be simply marked with concentric lines of growth,

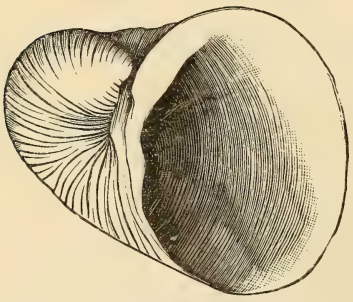
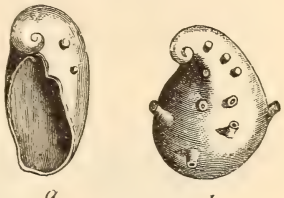


Fig. 646.—*Capulus* (*Platyceras*) *ventricosus*. Silurian. (After Hall.)

or may be ornamented with spines. The genus is abundantly represented in the Silurian and Devonian periods, and less abundantly in the Carboniferous; while ancient types have been described from the Upper Cambrian and Ordovician rocks. Many Secondary and Tertiary species are known, and the comparatively few living species are widely distributed over the globe.



a *b*

Fig. 647.—Different views of *Capulus* (*Platyceras*) *dumosus*, of the natural size. Devonian, Canada. (Original.)

According to Lindström, the name of *Platyceras* may be retained for the Silurian forms of *Capulus*, as presenting certain constant differences, and, in particular, as not having been clearly shown to possess the horse-shoe-shaped muscular scar of the latter. The same authority unites with *Platyceras* the Palæozoic types described under the names of *Platystoma* (Conrad) and *Strophostylus* (Hall). *Orthonychia*, again, includes forms with a nearly straight shell, the spire being very small, and the terminal portion of the shell very large.

Family 4. Velutinidæ.—The principal genus in this family is *Velutina*, in which the shell is thin, with a large body-whorl and small spire, and having a large rounded aperture with an entire margin. The genus is principally Recent and Tertiary, but a few Secondary types have been described.

Family 5. Pleurotomariidæ.—In this family the shell is nacreous, very variable in form, but usually coiled into an elevated or flat spiral. The outer lip of the shell-aperture (fig. 648) exhibits a notch or slit, which in course of growth becomes progressively filled up,

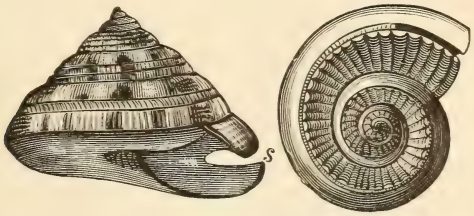


Fig. 648.—Side-view of the recent *Pleurotomaria Quoyana*, showing the slit in the outer lip (*s*); and upper view of *Pleurotomaria platyspira*, showing the slit-band.

thus giving rise to a revolving band upon the whorls; or which may become partially closed and converted into one or more perforations. The animal is provided with a circular horny operculum.

The family *Pleurotomariidæ* has relationships with the *Haliotidæ*, the *Bellerophontidæ*, and the *Euomphalidæ;* and the great majority of the genera included in it are extinct. If *Scissurella* be placed

among the *Trochidæ*, the only genus of the family which still survives is *Pleurotomaria* itself.

The genus *Pleurotomaria* is a "persistent type," the oldest forms appearing in the Upper Cambrian, while four living species have been detected. The genus is very largely represented in the Ordovician, Silurian, Devonian, and Carboniferous rocks. A very limited number of species has been hitherto obtained from the Permian deposits. In the Mesozoic rocks the genus again shows a great development, the Secondary forms being commonly more ornate than those from older rocks. Very few Tertiary species are known, and the few living species are found in the Antilles and in the Japanese seas.

Fig. 649.—*Pleurotomaria Agave.* Ordovician. (Billings.)

Fig. 650.—*Pleurotomaria Dryope.* Ordovician. (Billings.)

The form of the shell in *Pleurotomaria* (figs. 649, 650) differs considerably in different types, being most generally similar to that of *Trochus* or *Turbo*, but being in other cases very much flattened out and depressed. The shell consists of a few whorls, which are generally in close contact; but the last whorl may be disconnected from the others, or the shell may be entirely evolute (*Odontomaria*). The aperture of the shell is subquadrate, and the outer lip (fig. 648) exhibits a deeper or shallower slit. As the shell grows, this slit becomes progressively filled up, forming a well-marked band on the whorls. By this character *Pleurotomaria* may generally be distinguished readily from such shells as *Trochus* and *Turbo*.

Many subordinate types are included in the comprehensive genus *Pleurotomaria*, in the wide sense. Thus a number of Secondary types admit of separation from *Pleurotomaria* proper by their possession of a very deep slit and a narrow band, and these may be grouped together under the name of *Leptomaria*. In the Carboniferous *Polytremaria* the band on the whorls is partially obliterated, and is perforated by a linear series of minute foramina. In the Jurassic *Ditremaria* there is a kidney-shaped aperture, consisting of two foramina united by a slit, in the band near the outer lip. Lastly, in the Devonian *Odontomaria* the shell is tubular and evolute.

The Silurian genus *Euomphalopterus* is regarded by Lindström as an extreme form of *Pleurotomaria*. In this type the shell is a depressed spiral, the slit-band forming a wide alation, perforated by canals which

open into the cavity of the shell internally, and externally by minute pores on the margin of the wing. Again, in the Triassic and Jurassic genus *Trochotoma* (fig. 651, B) the shell is trochoid, with a concave base, and there is a single elongated perforation in the slit-band, near the margin of the outer lip. The ancient Ordovician types *Scalites*, *Rhaphistoma*, and *Helicotoma*, of which the two last are probably identical,

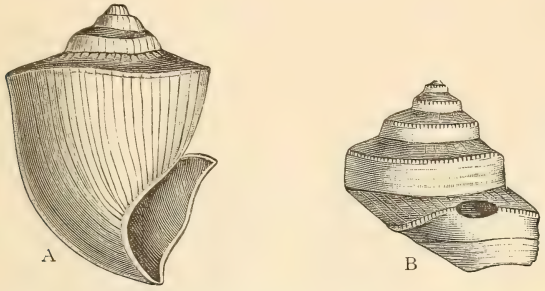


Fig. 651.—A, *Scalites angulatus*, Ordovician, North America. (After Hall.) B, *Trochotoma affinis*, Jurassic.

appear to be really referable to *Pleurotomaria*. In *Scalites* (fig. 651, A) the shell is spiral, with a flattened spire, the body-whorl ventricose, the "suture" canaliculated, the lip truncated, and the columella imperforate and curved. In *Rhaphistoma* the spire is still more depressed, the "suture" is close, instead of being grooved, there is an umbilicus of moderate size, and the aperture is somewhat trigonal and slightly notched.

The genus *Porcellia* (fig. 652), sometimes regarded as belonging to the *Bellerophontidæ*, seems to be really referable to the *Pleurotomariidæ*. In this genus the shell is discoidal and many-whorled, the outer lip having a deep slit, and the whorls having a well-marked revolving band running along the centre of the dorsal side. The species of *Porcellia* appear to range from the Devonian to the Trias.

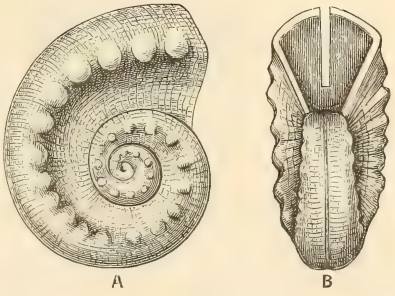


Fig. 652.—*Porcellia puzo*, viewed sideways (A) and from the front (B). Carboniferous.

Lastly, the important genus *Murchisonia* (fig. 653) is nearly related to *Pleurotomaria*, the line of separation between the two groups being, in fact, one which cannot be sharply defined. The shell in the typical forms of *Murchisonia* is long and turreted, the number of the whorls being greater

than in *Pleurotomaria*. The outer lip is deeply notched, and the outer side of the whorls shows the characteristic slit-band of the family. The aperture of the shell is slightly channelled in front, and the surface is often variously sculptured and adorned. The genus ranges from the Ordovician to the Permian rocks, and possibly is represented in the Alpine Trias.

Fig. 653.—*Murchisonia gracilis.* (Hall.) Ordovician.

Family 6. Bellerophontidæ.—In this family the shell (figs. 654, 655) is "nautiloid, generally symmetrical, spirally inrolled; the spire is concealed by the succeeding whorls; the aperture is of large size; the outer lip is arched, sharp-edged, simple, or greatly expanded, carrying in the middle line a sinus or notch, continued on the convexity of the last whorl by a slit-band or by a series of perforations" (Fischer). This family includes the extinct genus *Bellerophon* and its allies, and has been often referred to the order of the *Heteropoda*. The shell in *Bellerophon* is, however, of considerable thickness, and the genus is commonly found associated with forms which undoubtedly inhabited water of comparatively small depth. For these reasons, amongst others, the *Bellerophontidæ* can hardly be associated with a purely oceanic group such as the Heteropods. On the other hand, the presence of a dorsal revolving band on the whorls, and of a sinus or notch in the outer lip, brings the shell in relation with that of the

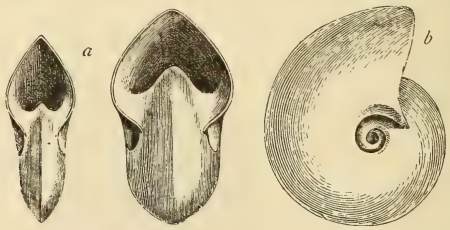


Fig. 654.—*Bellerophon Argo* (Billings). *a*, Front view; *b*, Side view. Ordovician.

Pleurotomariidæ; while an affinity with the *Haliotidæ* is established by the presence in some forms (*Tremanotus*) of a row of apertures on the dorsal keel of the shell. All the members of the *Bellerophontidæ* are extinct, and if the problematical Cretaceous genus *Bellerophina* be excluded, they are exclusively confined to the Palæozoic rocks.

In the genus *Bellerophon* (figs. 654, 655) the shell is symmetrically convoluted, the coils of the shell lying in one plane. The

whorls are few, smooth or sculptured, and there is a dorsal band or keel along the convex margin of the shell. The aperture is often more or less expanded, and is in most instances emarginate or deeply notched on the dorsal side, the columellar lip being generally more or less callous. The genus ranges from the Upper Cambrian to the Permian, but attains its maximum in the Carboniferous Limestone. *Bucania* (Silurian to Carboniferous) includes forms not generically separable from *Bellerophon*, but distinguished by the fact that all the volutions are visible and increase gradually in size

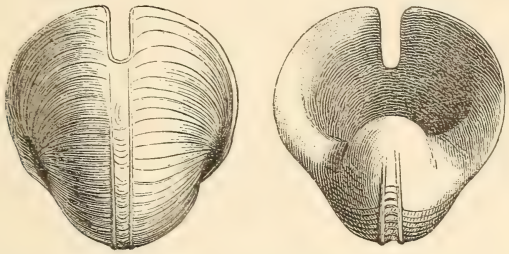


Fig. 655.—*Bellerophon bicarenus*, from the Carboniferous rocks of Belgium. (After Zittel.)

to the expanded mouth. The genus *Tremanotus* (Silurian) resembles *Bucania* in the form of the shell; but the dorsal band is replaced by a series of perforations which become successively filled up in process of growth, and which appear to correspond with the siphonal apertures in the shell of *Haliotis*. Closely allied to *Tremanotus* is the Silurian and Devonian genus *Salpingostoma*, in which there is a single elongated aperture on the dorsal margin of the body-whorl at some distance behind the margin of the lip.

In the neighbourhood of *Bellerophon* must also be placed the genus *Cyrtolites*, in which the shell is symmetrical, discoidal, or coiled into the shape of a horn, the whorls being in contact or more or less disconnected. The aperture is rhomboidal, with a median sinus, and a band or keel is developed on the convexity of the last whorl, while the surface is often sculptured. The genus ranges from the Ordovician to the Carboniferous.

Fig. 656.—*Cyrtolites ornatus*. Ordovician.

The affinities of the genus *Bellerophina*, of the Gault (Cretaceous), are quite uncertain, though it has often been associated with *Bellerophon*. The shell in this genus is globular, spirally inrolled, and nautiloid, but the outer lip has no sinus or notch, and the convexity of the whorls is not furnished with a keel or band. It is not improbable that this genus is really referable to the *Heteropoda*, but the structure of the shell is at present imperfectly known.

Family 7. Haliotidæ.—In this family the shell (fig. 657) is spiral and ear-shaped, nacreous internally, and with a large aperture. The body-whorl exhibits on the left side a series of rounded perforations, which become successively filled up, the last few, however, remaining always open. The last of these apertures corresponds with the anus and transmits a fold of the mantle, while the others give passage to tentaculiform prolongations of the pallial border. This family contains only the genus *Haliotis*, comprising the recent "Ear-shells." The oldest example of this genus is the *H. antiqua* of the Maestricht Chalk, and a few Tertiary species are known.

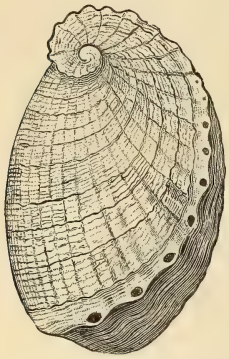


Fig. 657.—*Haliotis tuberculata*, from the Pliocene Tertiary.

Family 8. Stomatiidæ.—In this family the shell is spiral or ear-shaped, with a short spire, and an expanded entire aperture. The interior is nacreous, and the shell is destitute of the perforations which characterise *Haliotis*. The principal genus in this family is *Stomatia*, the earliest undoubted representatives of which appear in the Jurassic rocks, while others are Cretaceous and Tertiary, and a few forms still survive.

Family 9. Euomphalidæ.—As defined by De Koninck, the genera comprised in this family possess a spiral shell, sometimes elevated, sometimes discoid, the whorls being in contact or disjunct, and a larger or smaller umbilicus being present. The outer lip of the aperture exhibits one or two (rarely three) larger or smaller sinuses, of which the surface often shows only slight traces, except that their existence is usually marked by keels or by imbricated lamellæ of growth. The inner portion of the shell is often partitioned off by successively produced transverse septa; and a shelly operculum is sometimes present. Professor De Koninck includes in this family a number of extinct, mostly Palæozoic, genera, which are probably in some cases referable to different groups, but which will be here considered together, as a matter of convenience. On the other hand, none of the genera placed here by De Koninck are admitted into this family by Lindström except *Euomphalus* proper, while by this authority *Loxonema* is associated with *Euomphalus*.

The two principal types included in the *Euomphalidæ*, as defined by De Koninck, are *Straparollus* and *Euomphalus*, which many authorities have regarded as so nearly related as to have merely the standing of sub-genera, while Lindström considers them as belonging to entirely different families. In *Straparollus* (fig. 658) the shell is thick, typically conical, with a more or less prominent spire

and a large umbilicus, the whorls being rounded and non-angulated, the mouth round or oval, and the surface smooth or striated. The species of this genus range from the Silurian to the Trias. Apparently related to the preceding is *Platyschisma*, in which the shell is thin, obtusely conical, ventricose, umbilicated, and smooth, "with a shallow sinus in the outer lip, but with no defined band" (R. Etheridge, jun.) The genus appears to range from the Silurian to the Carboniferous.

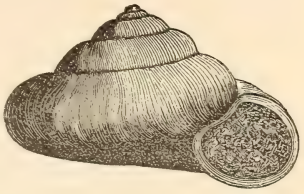


Fig. 658.—*Straparollus Dionysii*, from the Carboniferous Limestone of Belgium. (After Zittel.)

The genus *Euomphalus* (fig. 659), as defined by Lindström, comprises discoidal shells, in which the whorls are contiguous or disjunct; the umbilicus is wide; and the outer lip of the aperture possesses on its upper side a shallow notch or sinus, which gives rise to a more or less elevated revolving ridge or keel in the middle or upper part of the convexity of the whorls. The mouth of the shell is more or less angulated, while the apex is filled up with a secondary deposit of shell, and the interior is often divided off by transverse shelly partitions. The species of *Euomphalus* range from the Silurian to the Carboniferous, one of the most familiar types being the *E. pentangulatus* (fig. 659) of the Carboniferous Limestone. The well-known Silurian shells which have been described under the names of *Euomphalus discors* and *E. rugosus* have been shown by Lindström to have possessed a nacreous shell, and to be referable to the *Turbinidæ*.

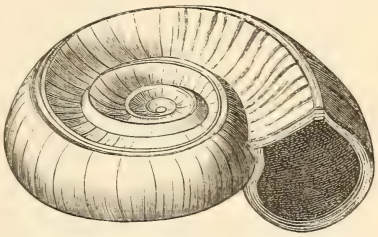


Fig. 659.—*Euomphalus pentangulatus*, of the natural size, from the Carboniferous Limestone of Ireland. (After Woodward.)

The name of *Schizostoma* is applied by De Koninck to forms with a shell (fig. 660) essentially similar to that of *Euomphalus*, as above described, but having two spiral keels, one on the upper and one on the lower aspect of the convexity of the whorls. It would seem that *Ophileta* is a synonym of *Schizostoma*, and in that case forms of this type range from the Ordovician to the Carboniferous. The forms to which the name of *Ecculiomphalus* has been applied (fig. 661) would appear, again, to be essentially identical with *Euomphalus*, from which they differ simply in the fact that the shell is evolute, the whorls not being in contact. Forms of this type are known to range from the Ordovician to the Carboniferous.

The name of *Cœlocentrus* (= *Cirrus*, De Koninck) is given by Zittel to certain Palæozoic types which have a general resemblance to *Euomphalus*, the shell being a flat spiral, with a large umbilicus (fig. 662). The shell differs from that of *Euomphalus* proper in the fact that the mouth is round, the outer lip is not sinuated, the

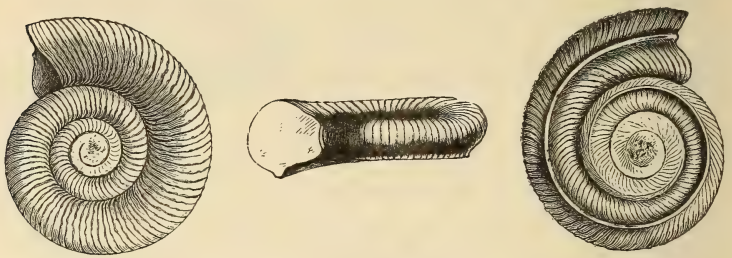


Fig. 660.—*Schizostoma* (*Ophileta*) *bella* (Billings). Different views of a nearly perfect specimen. Quebec Group (Ordovician).

whorls are more or less rounded, and the volutions support one or two rows of prominent spines.

Discohelix includes discoidal shells, concave on both faces, with the whorls flattened at the circumference, and furnished with two marginal keels, the aperture being quadrangular. Forms of this type appear to be principally characteristic of the Upper Trias and

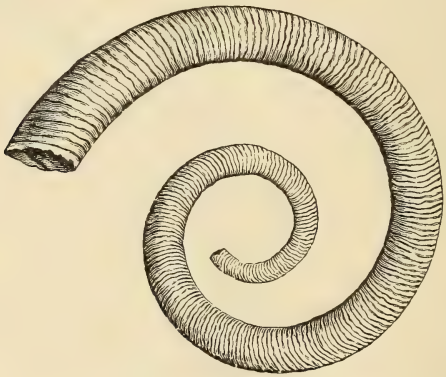


Fig. 661.—*Ecculiomphalus distans*. Quebec Group (Ordovician).

of the Jurassic rocks. *Bifrontia* (Eocene) appears to be nearly related to *Discohelix*.

The remarkable Palæozoic genus *Maclurea* (fig. 663) may be provisionally placed here; though its precise affinities are very doubtful, and it is regarded by Fischer as probably related to the

Neritidæ. In this genus the shell is discoidal, of few whorls, longitudinally grooved at the back, and ornamented with lines of growth.

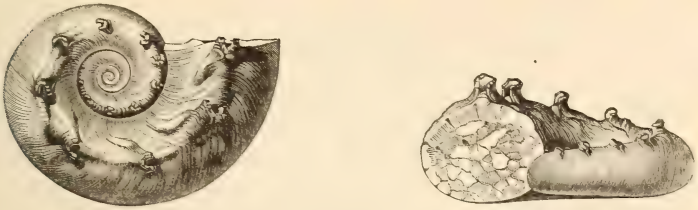


Fig. 662.—*Cœlocentrus* (*Cirrus*) *Goldfussi.* Devonian.

The upper side of the shell (drawn as the lower side in fig. 663, *b*) is convex, and deeply umbilicated by the sinking of the spire below

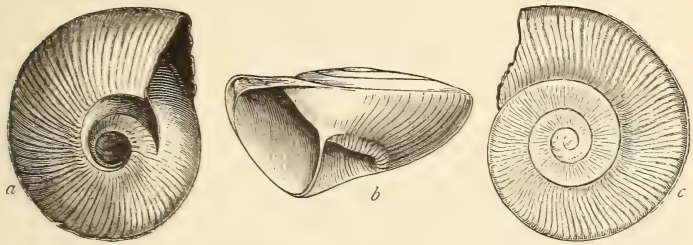


Fig. 663.—*Maclurea crenulata,* Ordovician (Quebec Group), Canada. *a,* Upper side, with the spire; *b,* Side view of the shell; *c,* Base. Properly speaking, figure *b* should have been drawn with the flattened base undermost and the hollow spire above. (After Billings.)

the general surface; while the base is flattened and exposes the inner whorls. The mouth of the shell is closed by a shelly operculum,

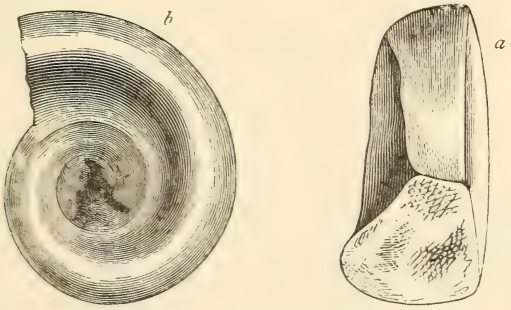


Fig. 664.—*Pleuronotus* (*Euomphalus*) *De-Cewi* (Billings). *a,* Front view; *b,* View of the umbilicus. Devonian, North America.

which is "sinistrally sub-spiral, solid, with two internal projections, one of them beneath the nucleus, very thick and rugose" (Woodward). The genus is essentially characteristic of the summit of the

Cambrian and the base of the Ordovician series (the Quebec Group and Chazy Limestone in North America, the Durness Limestone in Scotland, &c.)

Finally, we may notice here the Devonian fossil for which Billings proposed the name of *Euomphalus De-Cewi*, and upon which Hall has based the genus *Pleuronotus*. In this form (fig. 664) the shell is discoidal, with a wide shallow umbilicus and a concave spire, the outer lip of the aperture showing a distinct sinus. The surface on the summit and external side of the whorls is "marked by a distinct band, to the margins of which the surface-striæ converge on the two sides, and upon which they make a regular retral curve" (Hall). This last character renders it probable, as suggested by Hall, that *Pleuronotus* should be referred to the family of the *Pleurotomariidæ*.

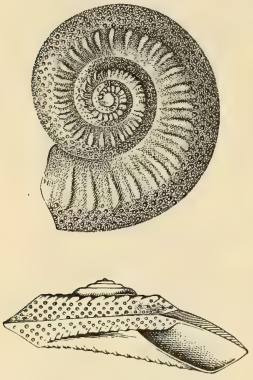


Fig. 665.—*Solarium ornatum*. Gault (Upper Cretaceous).

Family 10. Solariidæ. — In this family the shell is obtusely conical or depressed, with a large and deep umbilicus running from the base to the apex of the shell. There is no nacreous layer, and the aperture is entire. The principal genus in this family is *Solarium* itself (fig. 665), comprising the familiar "Staircase Shells." In this genus the edge of the umbilicus is typically crenulated, and the aperture is rhombic. The species of *Solarium* range from the Cretaceous (Trias?) to the present day.

Family 11. Trochidæ.—In this family the shell is conical, pyramidal, top-shaped, or helicoid, the aperture being entire, and either quadrilateral or round in form. The shell is *nacreous*, and the operculum is horny, circular, and multispiral, with a central nucleus. The members of this family are all marine, and are mostly found between tide-marks or in shallow water; a few forms, however, being inhabitants of deep water.

Fig. 666. — *Trochus conulus*. Pliocene Tertiary.

In the genus *Trochus* (fig. 666) the shell is pyramidal, with a nearly flat base, and the aperture is oblique and rounded in shape. The range of the genus is from the Silurian to the present day, but the determination of many of the fossil forms is uncertain, since it is by the structure of the operculum that the genus is essentially distinguished from *Turbo* and *Astralium*, and

opercula, even when shelly and massive, are not often met with in the fossil condition.

Monodonta in its general characters resembles *Trochus*, but the columella is thickened and carries a prominent tooth. The genus ranges from the Tertiary period to the present day, and doubtful representatives of it have been indicated as occurring in older times. In *Delphinula* the shell is orbicular and depressed, the whorls angulated or coronated, often spiny, the mouth round, the peristome entire, and the umbilicus open. The genus seems to begin in the Jurassic rocks. In *Umbonium* the shell is circular, with a short spire and a large body-whorl, the surface being polished, and the umbilical region covered with a prominent callosity. The genus begins in the Devonian, and still survives. Lastly, according to the views of Lindström, we must include in this family the genus *Scissurella* (fig. 667), in which the shell is thin, with a greatly expanded body-whorl, and the outer lip is furnished with a deep slit. The earliest forms of *Scissurella* appear in the Cretaceous rocks, and the genus still survives.

Fig. 667.—*Scissurella aspera.* Pliocene Tertiary.

Family 12. Turbinidæ.—The shell in this family is solid and nacreous internally (except in *Phasianella*), turbinated or trochoid in form, with an entire, round or oval aperture, and a rounded or flat base. The operculum is calcareous, paucispiral, with a central or excentric nucleus. The members of this family are marine, and inhabit shallow water.

In the genus *Turbo* (fig. 668) the shell is turbinated, with a round base, the whorls being convex, and the aperture large and rounded. The species of the genus range from the Silurian to the present day, about four hundred fossil species having been described; but owing to the non-preservation of the opercula there is much doubt as to the true position of many of the older forms.

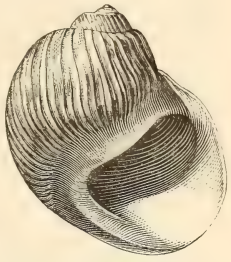


Fig. 668.—*Turbo subcostatus.* Devonian.

In *Astralium* (*Imperator*) the shell is trochoid, with a flat or concave base, and with keeled or foliaceous whorls and an angulated aperture. The genus ranges from the Trias to the present day. The genus *Oriostoma* (fig. 669) comprises Silurian and Devonian forms, in which the shell is discoid, with a short spire, the whorls being in contact, but the last whorl sometimes partially disjunct. The surface is usually spirally ribbed; there is a wide and open umbilicus; and the aperture has thin lips, without a sinus. The inner layer of the shell is nacreous, and there is a solid calcareous operculum. Some of the most familiar of the Silurian forms, such as *O. discors* (fig. 669), *O.*

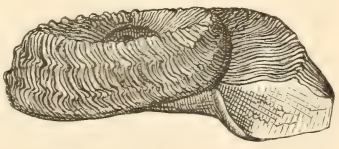


Fig. 669.—*Oriostoma* (*Euomphalus*) *discors.* Silurian, Britain.

rugosum, and *O. sculptum*, have been described as species of *Euomphalus*.

In *Cyclonema* (fig. 670, B) the shell is turbinated and imperforate, and the surface is adorned with raised spiral lines intersected by finer transverse striæ. The genus ranges from the Ordovician to the Devonian. The Devonian genus *Isonema* resembles *Cyclonema*, but the whorls are angular and the aperture is rhombic. In *Eunema* (fig. 670, A), again, the spire is elevated, the whorls are more or less angular, and the surface is adorned with elevated spiral ribs. The genus begins in the Ordovician, and the typical forms are Palæozoic. The Secondary genus *Amberleya*, however, seems to differ from *Eunema* principally, if not solely, in the fact that the spiral ribs are replaced or accompanied by rows of tubercles or nodosities. The Silurian and Devonian genus *Trochonema* resembles *Cyclonema*, but there is a wide umbilicus, bordered by an elevated ridge. In the Silurian genus *Craspedostoma* the shell is globular, the surface has transverse lamellar ribs, and there is a circular mouth "enclosed within an enormously enlarged and thickened border" (Lindström).

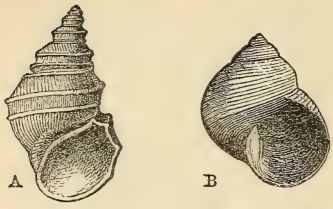


Fig. 670.—A, *Eunema strigillatum*, Ordovician (Trenton Limestone), Canada; B, *Cyclonema bilix*, Ordovician (Cincinnati Group), North America. (After Zittel.)

The genus *Phasianella* (fig. 671) represents another type of the *Turbinidæ*, in which the shell is not nacreous, and its surface is smooth and polished. The spire is long, the body-whorl is large, and the aperture is oval. The genus ranges from the Devonian to the present day.

Fig. 671.—*Phasianella melanoides*. Eocene Tertiary.

Family 13. Xenophoridæ.—This family includes only the genus *Xenophora* (*Phorus*), in which the shell (fig. 672) is trochoid, with a concave or flattened base and keeled whorls, but differs from that of the *Trochidæ* in not being nacreous. Very commonly, foreign bodies, such as shells or small pieces of stone, are attached to the surface and margins of the shell. The genus ranges from the Devonian to the present day.

Family 14. Neritidæ.—In this family the shell is thick and globular, with a very small spire, and without an umbilicus. The aperture is semilunate, its columellar side thickened and expanded, and often toothed (fig. 673), and the outer lip acute. There is a calcareous, sub-spiral operculum, provided with a process on its inner side. The "Nerites" are inhabitants partly of salt water and partly of fresh or brackish waters. In many cases the inner turns of the spire become absorbed in process of growth, so that casts of the interior of the fossil forms often show no traces of a spire.

In the genus *Nerita* (fig. 673) the shell is thick, with a broad columella, the inner edge of which is straight and toothed. The outer lip is thickened and often denticulated internally. The true Nerites are inhabitants of warm seas; and typical forms of the genus

Fig. 672.—*Xenophora* (*Phorus*) *canaliculata*. Cretaceous.

appear first in the Cretaceous rocks, though nearly related types are known from the Triassic and Jurassic rocks.

The Triassic and Jurassic genus *Neritodomus* closely resembles *Nerita*, but the columellar lip of the aperture is thickened and callous, and is without teeth. In the nearly allied *Neritoma*, of the Jurassic rocks, the shell is thick and ventricose, and the columellar lip is callous, and is not toothed, while there is a notch or sinus in the middle of the outer lip.

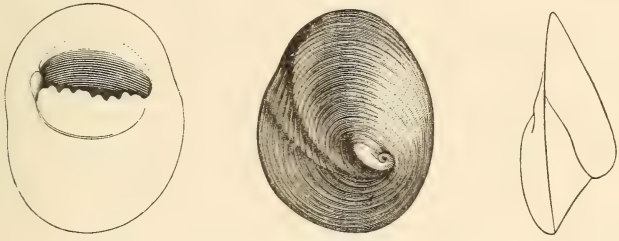


Fig. 673.—*Nerita* (*Velates*) *Schmideliana*. Eocene Tertiary.

The genus *Neritina*, again, includes the so-called "Fresh-water Nerites," which agree in most characters with *Nerita*, but inhabit fresh or brackish waters, and have a comparatively thin smooth shell. The oldest forms of *Neritina* seem to appear in the Lias, and the genus is abundantly represented in the fresh-water deposits of the Tertiary period, while many recent forms exist. Lastly, the genus *Pileolus* comprises small limpet-shaped shells, with a semilunar aperture. The range of the genus is from the Jurassic to the Eocene.

Family 15. Neritopsidæ.—In this family the shell resembles that of *Nerita* or *Natica* in shape, and is thick and imperforate. The aperture is entire, semilunate, or oval in form; and there is a thick shelly operculum, oval in shape, and non-spiral. In *Neritopsis* the shell is shaped like that of *Nerita*, of few volutions, and with a

short spire; and the columellar lip of the aperture is largely excavated about its middle. The genus ranges from the Trias to the present day. The name of *Peltarion* has been given to oval or nearly circular calcareous plates, concave above and flattened below, which are found in the Jurassic rocks, and which are now known to be the opercula of species of *Neritopsis*. Similar opercula occur in the Upper Trias and in the Tertiary rocks. The extinct genus *Naticopsis* (fig. 674) includes thick, imperforate, naticoid shells, with

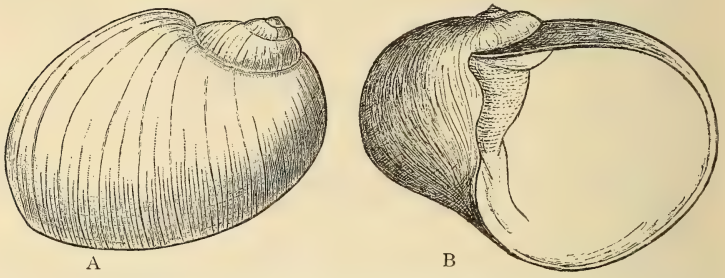


Fig 674.—A, *Naticopsis plicistria*, Carboniferous Limestone. (After M'Coy.) B, *Naticopsis ampliata*, Carboniferous Limestone. (After De Koninck.)

a short spire and a large body-whorl. The aperture is oval, and the columellar lip is callous and flattened, the outer lip being thin. A calcareous operculum is present. The genus ranges from the Devonian to the Upper Trias.

Family 16. Helicinidæ.—This family includes the recent *Helicina* and its allies, in which the shell is helicoid and globular, with a short spire, the interior turns of the spire being absorbed in course of growth. The aperture is semicircular, and a horny or calcareous operculum is present. This family has been generally included among the *Pulmogastropoda*, upon the ground that the breathing-organ is in the form of a pulmonary chamber, and the animal is terrestrial; but the true relationships of the group appear to be with the *Neritidæ*. All the undoubted forms of this family are Recent; but Fischer is inclined to place here the Carboniferous genus *Dawsonella*, which has been commonly included among the *Helicidæ*. In this genus the shell is like that of *Helix* in shape, with a small aperture, the outer lip of which is thickened, while the columellar lip is expanded into a large callosity, which covers the whole umbilical region.

Family 17. Naticidæ.—In this family the shell is globular, of few whorls, with a small spire (fig. 675); the aperture oval, rounded in front, and narrow behind, with an acute outer lip, and commonly with a callous inner lip. The foot is very large, and the mantle-lobes hide more or less of the shell. The operculum is pauci-

spiral, with an excentric nucleus, and may be either horny or calcareous.

The shell in *Natica* (fig. 675) is globular, with a large body-whorl, usually smooth and polished, and often with coloured markings. The inner lip is callous, and the shell is umbilicated, though the umbilicus may be partially or wholly filled up. A large number of recent, and a still larger number of fossil, forms of *Natica* are known, species having been described from rocks as old as the Silurian. It is, however, very questionable if any true forms of *Natica* are known from any Palæozoic deposit, anterior to the Carboniferous at any rate. The most typical forms of *Natica*, in a strict sense, possess a wide umbilicus and a twisted columella, and the oldest shells of this type are from the Eocene Tertiary.

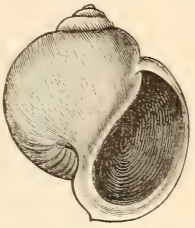


Fig. 675.—*Natica clausa.* Post-Pliocene.

Ampullina includes Eocene and Miocene forms, in which the columella is only slightly thickened and is not twisted. *Amauropsis* includes a number of fossil forms, of which the earliest perhaps appear in the Carboniferous Limestone, while many others are found in the Secondary rocks and the Eocene. In these types there is no umbilicus or only a narrow umbilical fissure, and the spire is moderately high. *Lunatia*, again, includes a series of forms, ranging from the Trias to the present day, in which the aperture is semilunar, and the umbilicus is of moderate or small size, and is without a spirally-twisted callus. The Eocene and Oligocene genus *Deshayesia* has the inner lip covered with a thick callosity, which largely conceals the umbilicus and is toothed on its apertural edge. The Jurassic and Cretaceous genus *Tylostoma*, lastly, includes forms with an elevated spire, and without an umbilicus, the outer lip being thin and sharp.

The genus *Narica* (*Vanikoro*) includes forms in which the shell has a general likeness to that of *Natica* (fig. 676), but the surface is spirally striated, or cancellated. The aperture is semilunate or oval, and the columella is excavated or umbilicated. The genus ranges from the Jurassic period to the present day. *Naticella* (Silurian to Trias) resembles *Narica*, but has no umbilicus or a small one. Lastly, in *Sigaretus* (fig. 677) the shell is ear-shaped, with a spirally-striated surface, a minute spire, and a very large

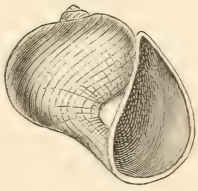


Fig. 676.—*Narica* (*Vanikoro*) *Genevensis*, from the Cretaceous rocks.

Fig. 677.—*Sigaretus clathratus*, from the Eocene.

body-whorl and wide aperture. The species of this genus are Tertiary and Recent.

Family 18. Paludinidæ.—In this family the shell is conical or globular, with a thick epidermis, and with convex whorls, the aperture being entire and sometimes furnished with a continuous lip The operculum may be horny or shelly. The members of this family are essentially fresh-water forms, though some are found in brackish waters, and *Ampullaria* is known in some cases to inhabit salt water. As a matter of course, therefore, they are chiefly, if not exclusively, found as fossils in deposits which are believed to be fluviatile, lacustrine, or estuarine in origin.

The genus *Vivipara* (*Paludina*) comprises forms with a conical shell, a generally smooth surface, and a horny operculum, an umbilicus being sometimes present, sometimes absent (fig. 678, A). The oldest forms of *Vivipara*, in the wide sense, are found in the Lower Cretaceous rocks (Wealden Beds), and a large number of Tertiary and Recent species are known. *Bithynia* resembles *Vivipara*, but the operculum is partially calcified; and its range in time is the same, though the known fossil forms are few in number. In *Valvata* (fig. 678, B) the shell may be top-shaped or discoidal; an umbilicus is present, and the peristome is entire. The earliest undoubted forms of this genus appear in the Upper Jurassic rocks (Purbeck Beds), and a small number of Tertiary and Recent forms are known. Lastly, in *Ampullaria* (fig. 639) the shell is globular, with a short spire and a ventricose body-whorl, and with or without an umbilicus. The operculum may be horny or calcareous. The geological range of *Ampullaria* is a matter of uncertainty, from the difficulty, or impossibility, of separating the shells of this genus from those of *Natica* and its allies. Forms from rocks as old as the Lias have been referred to *Ampullaria*, but it is doubtful if any representatives of the genus are known to occur in the fossil condition.

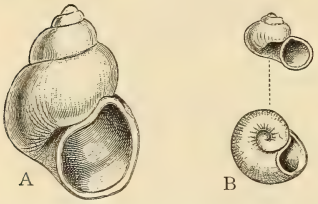


Fig. 678.—A, *Paludina lenta*, Pliocene; B, *Valvata piscinalis*, viewed from in front and from below. (After Searles Wood.)

Family 19. Rissoidæ.—In this family the shell is spiral, usually with an elevated spire, the aperture being entire and rounded, and the operculum horny and spiral. The members of this family are partly marine, partly inhabitants of brackish waters or marshes; and the two principal genera comprised in it are *Rissoa* and *Hydrobia*.

In the genus *Rissoa* (fig. 679) are included small, thick shells, generally more or less ribbed or striated, pointed in shape, many-whorled, and with a small round aperture surrounded by a continu-

ous peristome. The species of *Rissoa* are inhabitants of the sea, and the range of the genus in time is from the Jurassic to the present day. Forms of sub-generic value, or allied types, are *Rissoina* (Jurassic to Recent), *Keilostoma* (Chalk to Oligocene), *Diastoma* (Eocene), and *Pterostoma* (Eocene).

Fig. 679.—*Rissoa supracostata*, enlarged six times. Pliocene. (After Searles Wood.)

Hydrobia is nearly related to *Rissoa*, but the shell is usually thin and smooth. The species of this genus are mostly inhabitants of brackish or fresh waters, but a few live in the sea. The earliest forms of *Hydrobia* are recorded from the Jurassic rocks, but the genus is mainly Tertiary and Recent. The genus *Assiminea* differs from *Hydrobia* almost wholly as regards the animal, but forms are stated to occur in rocks as old as the Eocene.

Family 20. Littorinidæ. — In this family the shell is spiral, top-shaped, not nacreous internally, with a rounded and entire aperture and a simple thin outer lip. The operculum is horny and paucispiral. The members of this family are wholly marine; and their shells are very similar to those of the *Trochidæ* and *Turbinidæ*, except that there is no nacreous layer developed.

In the genus *Littorina* are the true Periwinkles, distinguished by their thick, generally top-shaped and pointed shells, of few whorls, and with an imperforate columella. The undoubted fossil species range from the Jurassic to the present day. In the Tertiary and Recent genus *Lacuna*, the shell resembles *Littorina* in most respects, but it is thin, and the columella is flattened and is bordered by an umbilical fissure. We may also include here the Silurian and Devonian genus *Holopea* (fig. 680), in which the shell is spiral, and either conical, or, more usually, naticoid, with a short spire and a large body-whorl. The surface is smooth or marked with faint transverse striæ; the outer lip is thin; the aperture is entire; and there may or may not be a narrow umbilicus.

Fig. 680. — *Holopea Guelphensis*. (Billings.) Silurian.

Family 21. Scalariidæ.—In this family the shell is spiral and turreted, many-whorled, the volutions marked with longitudinal ribs; and the aperture is round and furnished with a continuous peristome. The shell is perforated, but the umbilicus is often closed or concealed; and the operculum is horny and spiral.

In *Scalaria* itself are included the "Wentle-traps," in which the shell is elongated and many-whorled (fig. 681), and the volutions are adorned with transverse ribs, while the peristome is continuous round the circular aperture. The earliest forms of this genus

appear in the Trias, and a number of Jurassic and Cretaceous species are known; while the genus is largely represented in the Tertiary rocks and at the present day. In the Jurassic genus *Exelissa*, the essential characters agree with those of *Scalaria*, but the shell is of small size, the aperture is constricted, and the last whorl may be partially disjunct. The Triassic genus *Cochlearia* differs from *Scalaria* in having the whorls keeled and spirally striated, the transverse ribs being feebly or not at all developed, while the mouth is thickened and trumpet-shaped; and the Devonian genus *Scoliostoma* resembles *Cochlearia* except that the last volution is bent upwards and the surface is cancellated. Lastly, we may place here the ancient genera *Callonema* and *Holopella*, which agree with the typical members of this family in having a conical shell with an aperture surrounded by a continuous peristome. *Callonema* ranges from the Ordovician to the Devonian, and has the surface ornamented by remote, transverse, lamellar ribs; while in *Holopella* the ribs are reduced to mere striæ, or are obsolete.

Fig. 681.—*Scalaria Grœnlandica*. Post-Pliocene and Recent.

Family 22. Ianthinidæ.—The type of this family is the singular pelagic genus *Ianthina*, in which the shell is thin and turbinated, with an oval or subquadrate aperture, the outer lip being thin, and the columella slightly twisted. On the ground of similarity as regards the characters of the radula, *Ianthina* is placed by Fischer in the vicinity of the *Scalariidæ*. The only known fossil forms are from the Pliocene deposits of Italy.

Family 23. Turritellidæ.—In this family the shell is spiral, many-whorled, turreted, the surface spirally ribbed or striated. The aperture is round or subquadrate, entire, but sometimes slightly notched in front. The outer lip is thin, and the operculum is horny. All the members of this family are marine, and, if *Vermetus* and *Cæcum* be excluded, the principal representative of the group is *Turritella* itself (fig. 682), the characters of which are therefore those given above. Many living *Turritellæ* are known, and a still larger number of fossil forms have been described, the earliest unquestionable representatives of the genus occurring in the Jurassic, or perhaps in the Triassic deposits. Most of the fossil species, however, are found in the Tertiary rocks.

Family 24. Vermetidæ.—In this family the shell (fig. 683) is tubular, more or less spiral at first, but with its last turns disjunct. The aperture is round, and is entire or furnished with a lateral slit. A horny circular operculum is usually present. All the members of

this family are marine, and the two principal types are *Vermetus* and *Siliquaria*. The genus *Vermetus* is remarkable for the resemblance of its tubular shell to the calcareous tubes of *Serpula*. The shell is usually attached to some foreign body, and though regularly spiral when young, is always irregular in its growth when adult. The fossil species are best distinguished from *Serpula* by the fact that the tube is repeatedly partitioned off by calcareous septa as the animal grows. It is, however, often a matter of extreme difficulty to determine whether a given specimen be a *Vermetus* or a *Serpula*. The range of *Vermetus* in time, using this name in its wide sense, is from the Carboniferous period to the present day; but most of the fossil forms belong to the later Secondary and Tertiary deposits. In the

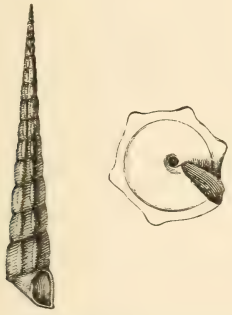


Fig. 682.—*Turritella angulata*. Neocomian.

Fig. 683.—*Siliquaria anguina*. Pliocene and Recent.

genus *Siliquaria* (fig. 683) the shell resembles that of *Vermetus* in most respects, but it is free, and the tube has a continuous longitudinal slit, which may be replaced by a row of pores, running along the whole length of the shell on one side. The genus ranges from the Cretaceous to the present day.

Family 25. Cæcidæ.—This family comprises only the genus *Cæcum*, in which the shell is free, and, to begin with, forms a small flat spiral. With age, however, the shell becomes decollated, and has in its adult state the form of a curved cylindrical tube, the truncated end of which is closed by a transverse calcareous partition. A number of recent and a few fossil forms of the genus are known, the oldest of the latter being found in the Eocene Tertiary.

Family 26. Pyramidellidæ.—In this family the shell is spiral and turreted, often with a polished surface. The aperture is small and entire, sometimes with one or more prominent plaits on the columella. The operculum is horny, ear-shaped, and paucispiral. All the members of this family are marine, and most of the living forms are of small size.

In *Pyramidella* (fig. 684, B) the shell is slender and turreted, and the columellar lip is plaited. The genus is represented by a number of Recent and Tertiary species, while still older forms occur in the Cretaceous rocks. *Odostomia*, with a similar geological range, includes minute turreted shells very similar in most respects to *Pyramidella*, but having a single tooth-like columellar fold. *Turbonilla*, with the same range in time, nearly resembles the preceding, but the columellar lip is simple, or has a feeble oblique fold. *Chemnitzia* (fig. 684, C) includes a number of slender, turreted, many-whorled shells, with plaited whorls and a simple aperture, the columellar lip having neither teeth nor folds. Numerous fossil forms are known in the Triassic, Jurassic, and Cretaceous deposits, in marine sediments only; and there are also Tertiary species. It is doubtful if the distinction between *Chemnitzia* and *Turbonilla* can be maintained. *Eulima* (fig. 684, A) includes small, polished, elongated shells, with level whorls and a reflected inner lip. The genus ranges from the Trias to the present day, a large number of species occurring in the Tertiary deposits. *Niso*, with the same geological range, has the shell umbilicated, but otherwise resembles *Eulima*.

Fig. 684.—A, *Eulima vagans*, Jurassic (after Morris and Lycett); B, *Pyramidella læviuscula*, Pliocene (after Searles Wood); C, *Chemnitzia internodula*, Eocene (after Searles Wood).

Fig. 685.—*Loxonema rugifera*, Carboniferous Limestone. (After Phillips.)

Family 27. Pseudomelaniidæ.—This family has been founded for the reception of certain extinct marine Gastropods, of which *Loxonema* and *Macrocheilus* are the two most important types. In this family the shell is many-whorled and turreted, with an oval aperture, which is typically entire, but is occasionally notched in front. The columella is simple, or may be slightly folded anteriorly. The forms included in this family have a general resemblance to *Melania*, but they are found in deposits of marine origin, whereas the *Melaniæ* are inhabitants of fresh water.

The shell in *Loxonema* (fig. 685) is long and turreted, with convex whorls, which have no spiral band; and the surface is covered with longitudinal, often more or less arched striæ or ribs, while the outer lip is more or less sinuated. The genus ranges from the

Silurian to the Trias, but attains its maximum development in the Carboniferous Limestone.

The genus *Macrocheilus* (fig. 686) includes thick smooth shells, with a moderately long spire and a pointed apex, and with convex whorls. The aperture is oval, not distinctly notched; the inner lip is callous, and the columella is imperforate and obtusely folded in front. The genus ranges from the Devonian to the Trias, the majority of the known species being Carboniferous. No species of the genus has been detected in the later Secondary or Tertiary deposits, but a living Japanese shell has been referred here. The Devonian and Carboniferous genus *Orthonema* appears to be related to *Loxonema*, and the Carboniferous genus *Soleniscus* has been placed here, though the aperture is canaliculated in front. Lastly, the Secondary and Tertiary genus *Pseudomelania* finds a place in this family.

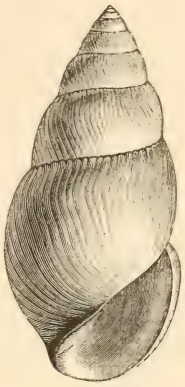


Fig. 686.—*Macrocheilus arculatus*. Middle Devonian.

Family 28. Melaniidæ. — In this family the shell is spiral and turreted, covered with a thick epidermis, and often much eroded towards the apex of the spire. The aperture is oval, and either entire or channelled or notched in front (fig. 687), the outer lip being acute. The operculum is horny and spiral. The members of this family are essentially fresh-water Gastropods, a few forms only inhabiting brackish waters.

In *Melania* itself the shell is usually adorned with striæ, ribs, or spines, and the aperture is entire and pointed above (fig. 687, A). The recent species of *Melania* have an exceedingly wide geographical range, and fossil forms are found in moderate numbers in the Cretaceous and Tertiary deposits. In *Pleurocera* the aperture is canaliculated below, and the outer lip is sinuated. The recent forms of this type are North American, and the genus has numerous representatives in the Cretaceous and Tertiary deposits. In *Melanopsis*, lastly, the aperture is deeply notched, and the spire is often shortened; while in *Pirena* (fig. 687, C) the aperture has the same form, but the shell

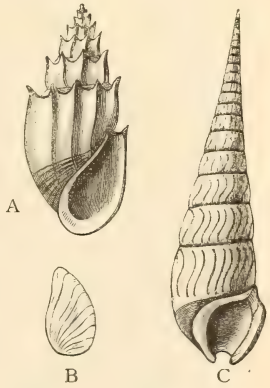


Fig. 687.—A, *Melania amarula*, and (B) its operculum, Recent; C, *Pirena atra*, Recent. (After Woodward.)

is turreted. Both genera range from the Cretaceous period to the present day.

Family 29. Cyclostomidæ.—In this family are included terrestrial Gastropods, which possess a pulmonary chamber, and which have therefore been commonly included among the *Pulmogastropoda*. The shell is of variable shape, spiral, sometimes conical (fig. 688), sometimes depressed or discoidal. The aperture is nearly circular, and the peristome is simple or reflected. An operculum is present, and is usually more or less extensively calcified. The principal genus in this family is *Cyclostoma* (fig. 688) itself, which has been split up into a number of subordinate groups. The oldest forms of *Cyclostoma*, in the general sense, appear in the Cretaceous rocks, and a number of Tertiary species are known, while the genus is largely represented at the present day.

Fig. 688. — *Cyclostoma Arnoudii*. Eocene Tertiary.

Family 30. Aciculidæ.—This family includes small terrestrial Gastropods, provided, like the preceding, with a pulmonary chamber. The shell is elongated and cylindrical, with a blunt apex, and a thickened peristome. There is an operculum, but this is never calcified. The recent genus *Acicula* is represented in the later Tertiary deposits.

The genus *Truncatella* — sometimes regarded as the type of a separate family (*Truncatellidæ*) — comprises littoral or fresh-water Gastropods, sometimes semi-terrestrial in habit, and related on the one hand to *Acicula*, and on the other hand to the *Rissoidæ*. The nature of the breathing-organs has not been clearly ascertained. The shell in *Truncatella* is elongated and cylindrical, often truncated in the adult state, and with an entire oval aperture. Species of the genus have been detected in the Tertiary deposits, the oldest appearing in the Eocene.

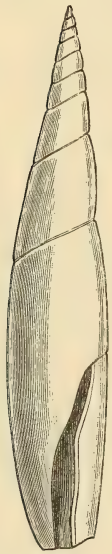


Fig. 689.—*Subulites terebriformis*, Silurian, North America. (After Hall.)

Family 31. Subulitidæ.—In this family the shell (fig. 689) is elongate and fusiform, with a smooth surface. The aperture is long and narrow, and is distinctly canaliculated in front. This family includes some Palæozoic and Triassic Gastropods, of which *Subulites* is the type, in all of which the peristome is incomplete and the shell notched in front. By Lindström the members of this group are regarded as the most ancient representatives of the division of the Siphonostomatous Prosobranchs.

In *Subulites* (? = *Polyphemopsis*, Portlock) the shell is elongated, slender and fusiform, with a smooth surface and a shallow suture. The shell is thin and fragile, and is truncated or rounded in front (fig. 689). The aperture is long and narrow; the outer lip is thin, and the inner lip is involute; and there is a distinct notch in front. The range of the genus is from the Ordovician to the Carboniferous. The genus *Euchrysalis*, ranging from the Silurian to the Trias, closely resembles *Subulites* in the shape and other characters of the shell, and is, perhaps, hardly separable from the preceding. Lastly, in the Ordovician genus *Fusispira* (fig. 690) the shell is fusiform, with an elevated spire and convex whorls. The aperture is oval or elliptical, and is prolonged below into a shallow canal; while the columella is twisted, but is without folds.

Fig. 690.—*Fusispira terebriformis*. Ordovician. North America. (After Hall.)

Family 32. Nerineidæ.—In this family the shell is turreted, thick, and solid, and the aperture is canaliculated in front. The outer lip is acute, and is sinuated superiorly or posteriorly, a slit-band which runs continuously below the suture being thus produced. The columella and parietes of the aperture are furnished with continuous folds, which are prolonged into the interior of the spire. All the members of this family are extinct, and all are confined to the Secondary period.

Fig. 691.—*Nerinea bisulcata*. Chalk. In the lower part of the specimen the shell is preserved, while the upper part shows the cast of the interior.

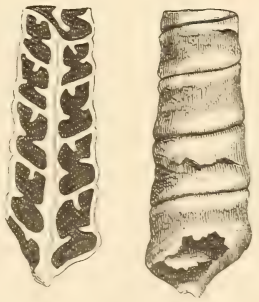


Fig. 692.—*Nerinea Goodhallii*, one-fourth of the natural size. The left-hand figure represents a vertical section of the shell. Coral Rag, England.

The principal or sole genus in this family is *Nerinea* itself, which has been divided into several sub-genera. In this genus the shell (figs. 691 and 692) is turreted, many-whorled, and nearly cylindrical. The columella carries continuous ridges, and similar ridges exist on the interior of the whorls, so that casts of the interior are often very unlike the exterior. The genus *Nerinea* is wholly Jurassic and Cretaceous, a very large number of species being found in the former of these systems, and particularly in strata of the age of the Coral Rag.

Family 33. Cerithiidæ.—In this family the shell (fig. 693) is spiral and turreted. The aperture is oval or quadrate, and is channelled in front, the canal being short and often bent backwards. The outer lip is generally expanded in the adult, the columella is sometimes thickened, and the operculum is horny and spiral. The members of this family are marine or live in brackish waters, some forms frequenting salt marshes or the mouths of rivers. More than three hundred recent species, and over a thousand fossil forms, of this family have been described, the most ancient types appearing in the Trias. The known forms belong to the two comprehensive genera *Cerithium* and *Potamides*, each of which has been split up into minor groups, to some of which a generic value is sometimes attached.

In *Cerithium* proper (fig. 693) the shell is without an epidermis, the operculum is paucispiral, and the aperture has a well-developed, backwardly-bent canal. The species of *Cerithium* are essentially marine, and the genus has been broken up into sub-generic groups (*Fibula*, *Eustoma*, &c.), the distinctive characters of which are mostly of small importance. The species of *Cerithium* abound in the Secondary and Tertiary rocks, and in warm seas at the present day. The oldest forms appear in the Alpine Trias.

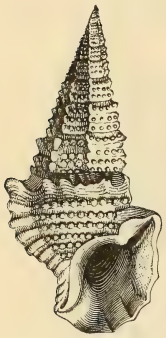


Fig. 693.—*Cerithium hexagonum.* Eocene Tertiary.

The genus *Potamides* closely resembles *Cerithium* in general characters; but the surface is covered with epidermis, the aperture has only a short canal or a notch in front, and the operculum is multispiral. The species of *Potamides* live in brackish waters or at the mouths of rivers. In the fossil condition the shells of *Potamides* cannot be certainly distinguished from those of *Cerithium*, but it is usual to consider that the representatives of this family which occur in estuarine or fresh-water deposits are referable to the former genus, while those which occur in purely marine deposits belong to the latter. On this view, the species of *Potamides* are Cretaceous, Tertiary, and Recent.

The genus has been split up into several sub-genera (*Bittium*, *Triforis*, *Ceritella*, &c.), but these are of little importance.

Family 34. Aporrhaidæ.—In this family the shell is fusiform, turreted or conical; the aperture is prolonged in front into a canal; the outer lip is expanded, aliform or digitate; and the operculum is horny. The members of this family are all marine, and they are closely allied to the *Strombidæ*. The two principal genera in this family are *Aporrhais* itself and *Alaria*.

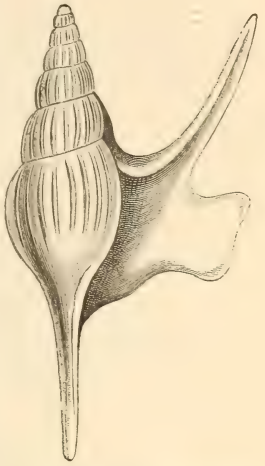


Fig. 694.—*Aporrhais Parkinsoni*. Cretaceous. (After J. Starkie Gardner.)

In *Aporrhais* (fig. 694) the shell is spindle-shaped, with a turreted spire, and the outer lip of the adult is greatly expanded and lobed, the inner lip being callous. The aperture is narrow, and is prolonged into a longer or shorter anterior canal, while its posterior angle is prolonged into an open tube, and the outer lip is sinuated in front. The genus has been broken up into numerous minor groups, and is represented by numerous Jurassic, Cretaceous, and Tertiary forms, and by a few recent species. The genus *Alaria* comprises forms with a general resemblance to *Aporrhais*; but there is no posterior canal, and the outer lip has no proper sinus in front. The species of *Alaria*, in the wide sense of the name, are confined to the Jurassic and Cretaceous deposits, being especially abundant in the former.

Family 35. Strombidæ.—In this family the shell is conical or fusiform, with a pointed spire. The aperture is prolonged into a canal in front; and the outer lip is expanded, and has a notch or sinus in front, near the canal. The operculum is horny and claw-shaped. The foot is narrow and adapted for leaping, and there is a long proboscis, with two tentacles carrying the eyes at their apices. The members of this family are all marine.

In the genus *Strombus* the shell has a short spire and a large body-whorl, and the long aperture is prolonged into a short canal in front and has a notch behind. The outer lip is expanded, and is more or less deeply indented or notched in front, near the canal. The genus is represented by a number of recent species, and by a moderate number of Cretaceous and Tertiary species.

The genus *Pteroceras* (or *Pterocera*) comprises the so-called "Scorpion-shells," in which the shell of the adult (fig. 695) has its outer lip furnished with long claws, one of which forms a posterior

canal close to the spire. Many fossil species are known, commencing in the Lias.

In the genus *Rostellaria* (fig. 696), the spire is long, and has the posterior canal running up it. Many fossil species are known, commencing in the Cretaceous rocks. The outer lip is always expanded, and in some forms is enormously so. One of the most familiar species is the great *R. ampla* (fig. 696) of the London Clay (Eocene).

Lastly, in the genus *Terebellum* (=*Seraphs*) the shell is elongated and subcylindrical, with a short or obsolete spire. The aperture is long and narrow, with a thin outer lip and a short canal. There is

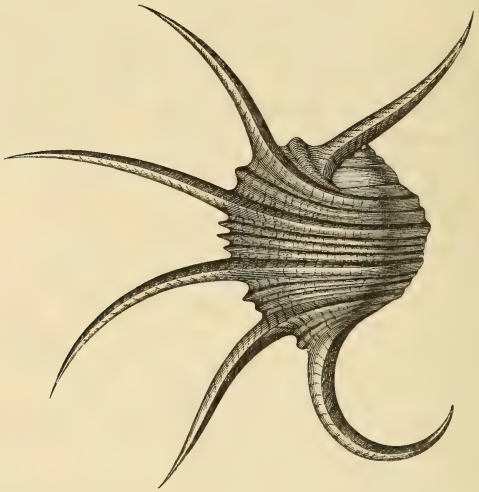


Fig. 695.—*Pteroceras oceani.* Neocomian.

an emargination of the outer lip in front. The genus is Tertiary and Recent, most of the fossil forms being found in the Eocene rocks.

Family 36. Cypræidæ. — In this family the shell is spirally rolled up, but the spire is more or less completely concealed, owing to the fact that the shell becomes overlaid by a coating of enamel. The aperture is long and narrow (fig. 697), and is channelled at both ends. The outer lip is thin in the young shell, but is thickened and strongly inflected in the adult. The foot is broad, and the mantle forms lobes which meet over the back of the shell.

The principal genus in this family is *Cypræa* itself, comprising the numerous and well-known living shells commonly spoken of as Cowries. The *Cyprææ* are mainly, but not exclusively, inhabitants of warm seas, and they attain their highest development

between the tropics. A single species has been found in the highest Jurassic beds in Sicily (Zittel), but with this exception the

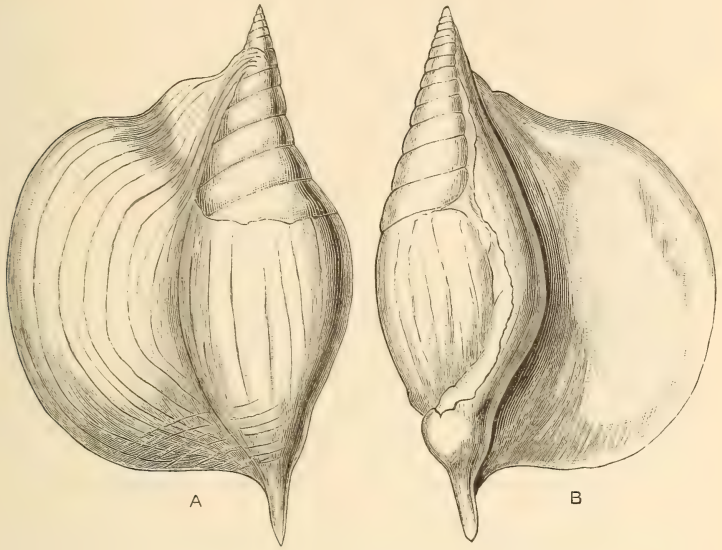


Fig. 696.—*Rostellaria ampla*, reduced one-third. Eocene Tertiary.

fossil species date from the Cretaceous period, and abound in the Tertiaries.

The shell of the Cowries in the young state is furnished with a prominent spire, and has a thin outer lip. In the adult state (fig. 697) the spire is completely concealed within the shell, the entire surface is generally covered with shining enamel, the inner lip is crenulated, and the outer lip is thickened, inflected, and crenulated. The small Cowries of which the common *Cypræa* (*Trivia*) *Europœa* is the type, are not known to occur in the Secondary rocks, but have a few Tertiary representatives. They are distinguished from the ordinary Cowries by the fact that the upper surface is adorned with transverse ribs. The genus *Ovulum* is closely related to *Cypræa*, but the aperture is drawn out anteriorly and posteriorly, and the inner lip is smooth. The genus dates from the Eocene, and possesses a number of existing representatives. *Erato*, again, ranging from

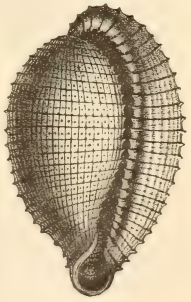


Fig. 697.—*Cypræa elegans*. Eocene Tertiary.

the Chalk to the present day, differs from the Cowries in having a cone-shaped shell, with a short but visible spire.

Family 37. Cassididæ.—In this family the shell is ventricose, with a short spire and a large body-whorl. The aperture is long and narrow, notched in front, or with a short recurved canal (fig. 698). The inner lip is callous, and the outer lip is thickened and often plaited or denticulated. The members of this family are all marine, and the oldest forms belonging to it appear in the Upper Cretaceous rocks.

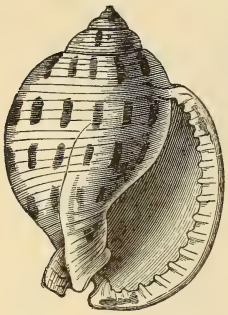


Fig. 698.—*Cassis canaliculatus.* Recent.

The genus *Cassis* (fig. 698) comprises the "Helmet-shells," distinguished by their short spire, large body-whorl, elongated aperture, short recurved anterior canal, and expanded inner lip. The earliest forms of *Cassis* appear in the Eocene Tertiary, and the genus still survives. *Cassidaria* (Upper Cretaceous to Recent) closely resembles *Cassis*, but the canal is elongated and produced. Lastly, *Oniscia*, with the same range in time as *Cassidaria*, has the aperture truncated in front, with a straight canal or notch.

Family 38. Doliidæ.—In this family the shell is thick and ventricose, with a large body-whorl and a wide oval aperture. The whorls are longitudinally ribbed, and there is a short anterior canal, which may be straight or recurved. This family includes only the genus *Dolium*, the species of which are marine. The fossil forms are chiefly Tertiary, but a Cretaceous species of the genus is known.

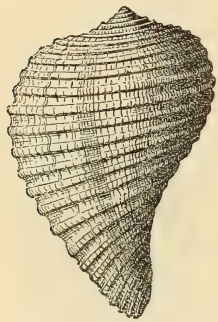


Fig. 699.—*Ficula* (*Pyrula*) *reticulata.* Miocene Tertiary. (After Zittel.)

Family 39. Ficulidæ. — In this family the shell is thin and ventricose, spirally ribbed or cancellated (fig. 699). The aperture is of large size, and is prolonged in front into a long canal. This family includes only the genus *Ficula* (*Pyrula* in part), in which the shell is pyriform, with a very large body-whorl and a short spire, and with a sharp outer lip. The recent species of *Ficula* are inhabitants of the sea, and the earliest fossil forms of the genus appear in the Cretaceous rocks.

Family 40. Tritoniidæ.—In this family the shell is spindle-shaped, with a straight or somewhat bent canal. The whorls are often adorned with varices, and a horny operculum is present.

The members of this family are all marine, and the two principal genera contained in it are *Tritonium* (= *Triton*) and *Ranella*. The former of these ranges from the Cretaceous period to the present day, while the species of the latter are Tertiary and Recent.

Family 41. Buccinidæ.—In this family the shell is conical, with a large aperture, which is notched in front, or prolonged into a very short canal, which is reflected so as to produce a sort of varix on the back of the shell anteriorly. All the members of this family are marine, and the three most important genera comprised in it are *Buccinum*, *Nassa*, and *Eburna*.

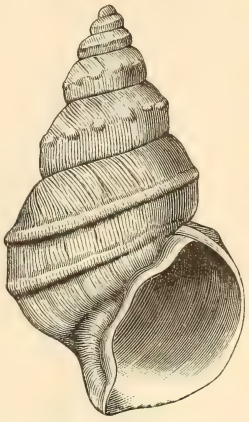


Fig. 700.—*Buccinum glaciale*. Post-Pliocene and Recent.

The Whelks form the genus *Buccinum* (fig. 700), distinguished by the ventricose body-whorl, large aperture, and short reflected canal. Some few species of *Buccinum* are found in the Cretaceous rocks; but the genus is essentially Tertiary and Recent.

The genus *Nassa* (fig. 701) comprises the "Dog-whelks," in which the shell has a general resemblance to that of *Buccinum*, but the columellar lip is expanded and callous, and generally shows a tooth-like fold near the anterior canal. More than two hundred recent species of *Nassa* are known, and a large number of Pliocene and Miocene species have been described. In the early Tertiary deposits the genus is sparingly represented, and the oldest types appear in the Chalk.

Fig. 701. — *Nassa pusillina*. Pliocene. (After Searles Wood.)

In the genus *Eburna*, the shell is umbilicated when young, but the inner lip is callous, and in the adult condition is expanded so as to cover the umbilicus. The genus is wholly Tertiary and Recent. Lastly, the genus *Brachytrema* includes Jurassic types of the *Buccinidæ*, in which the shell is turbinated, solid, and of small size, with nodulated, ribbed, or cancellated whorls. The columella is smooth, and there is a short oblique canal. By Fischer the genus is doubtfully referred to the *Cerithiidæ*.

Family 42. Columbellidæ.—In this family the shell is ovate or fusiform, with a short spire and a large body-whorl. The aperture is long and narrow; the outer lip is thickened and toothed internally, and the inner lip is toothed or granulated in front. The members of this family are all marine, and the three principal genera

comprised in it are *Columbella* (Tertiary and Recent), *Columbellina* (Cretaceous), and *Columbellaria* (Jurassic and Cretaceous).

Family 43. Purpuridæ.—In this family the shell is oval or fusiform, with a short spire. The columellar lip is expanded and more

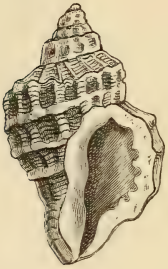


Fig. 702.—*Purpura tetragona.* Pliocene. (After Searles Wood.)

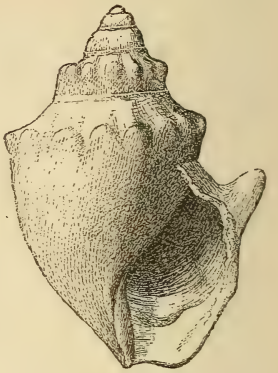


Fig. 703.—*Purpuroidea nodulata.* Jurassic. (Copied from Zittel.)

or less flattened, and there is a short anterior canal. The members of this family are all marine, and the principal genera are *Purpura*, *Purpuroidea*, and *Rapana*.

In the genus *Purpura* (fig. 702) the shell has a short spire and a large body-whorl; the columellar lip is smooth and flattened;

Fig. 704.—*Fusus Neocomiensis.* Lower Greensand.

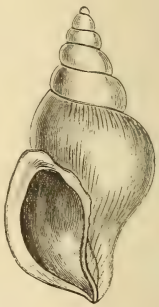


Fig. 705.—*Fusus* (*Chrysodomus*) *contrarius.* Pliocene (Red Crag).

and there is a short oblique canal or notch in front. The genus is exclusively Tertiary and Recent, and the fossil forms are few in number.

In the Jurassic and Cretaceous genus *Purpuroidea* (fig. 703) the shell is oval and ventricose, with a short pointed spire and a large

body-whorl. The whorls are convex and have a row of tubercles below the suture. The outer lip is thin, the columella is smooth, and there is a short wide canal. Lastly, in *Rapana* the shell is ventricose, with a short spire, the aperture is produced in front, and the columella is umbilicated. The genus ranges from the Cretaceous to the present day.

Family 44. Fusidæ.—In this family the shell is elongated or fusiform, dextral, or sinistral, usually without varices. The aperture is moderately long, and is produced in front into a long straight canal. The operculum is horny. The members of this family are all marine, and the principal genera placed under this head by Zittel are *Fusus*, *Pisania*, *Fasciolaria*, *Turbinella*, and *Pyrula*.

In the genus *Fusus* the shell is spindle-shaped (figs. 704 and 705) and many-whorled, with an elongated straight canal. A very large number of Recent and fossil forms of *Fusus* have been recorded, and the genus has been broken up into a large number of minor groups or sub-genera, the characters of which cannot be discussed here. Using the term in its wide sense, *Fusus* ranges from the Jurassic period to the present day, attaining its maximum development in the Eocene and Miocene periods. An abundant form in the Red Crag (Newer Pliocene) is the well-known *Fusus* (*Chrysodomus*) *contrarius*, in which the shell is reversed (fig. 705). This species has now been found in the living condition. *Fusus* (*Chrysodomus*) *tornatus* is a common fossil in the Glacial deposits of Canada (fig. 706), and still survives in the neighbouring seas.

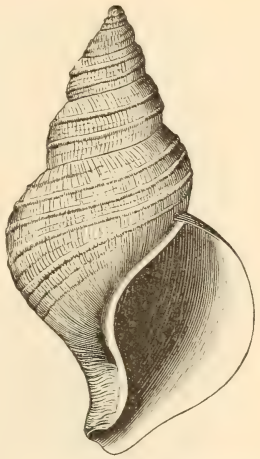


Fig. 706.—*Fusus* (*Chrysodomus*) *tornatus*, from the Glacial deposits of Canada.

In *Pisania* the shell is generally of small size, with an elevated spire and a short canal. The surface is smooth or spirally striated, and the outer lip is crenulated. The genus is exclusively Tertiary and Recent.

In *Fasciolaria* the shell is fusiform and elongated, with smooth, angulated, or tuberculated whorls. The aperture is elongated, and is prolonged anteriorly into a wide, generally straight canal. The outer lip is thin, and the columellar lip is tortuous, with several oblique folds. The genus ranges from the Chalk to the present day.

In *Turbinella* the shell is thick, with a short spire and a long straight canal, the columella having several transverse folds. Lastly,

the genera *Melongena*, *Fulgur* (fig. 707), and *Tudicla*, form portions of the old genus *Pyrula*, and all possess a pear-shaped ventricose shell, with a short spire and a large body-whorl. *Melongena* has a short wide canal and nodose or spinose whorls, and is exclusively Tertiary and Recent. *Fulgur* and *Tudicla*, on the other hand, have a long straight canal; and both genera have recent representatives, the former commencing in the Miocene, and the latter in the Cretaceous deposits.

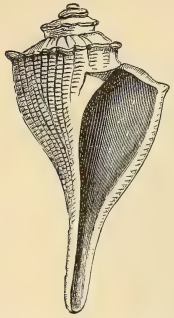


Fig. 707. — *Fulgur canaliculatus*. Miocene.

Family 45. Muricidæ.—In this family the shell has a moderately high spire, and the surface is adorned with foliaceous expansions, spines, or well-marked varices. The aperture is round or oval, entire posteriorly, and prolonged anteriorly into a straight or slightly oblique canal, which is generally partially closed in. The members of this family are all marine, and with the exception of a few Cretaceous forms, they are confined to the Tertiary and Recent periods.

In the genus *Murex* (fig. 708) the shell is sometimes elongated, sometimes ventricose, and the surface is adorned with varices in the form of longitudinal ridges or rows of spines. The aperture is rounded, and the canal is usually greatly prolonged, and is always partially closed in. Taken in its wide sense, the genus *Murex* ranges from the Chalk to the present day, a large number of species having been obtained from the Tertiary rocks. In the nearly related genus *Typhis* (fig. 709) there are tubular spines between the varices, and the last of these lodges the posterior siphon, while the canal is completely closed in. The species of *Typhis* range from the Chalk to the present day. Lastly, in the genus *Trophon* the shell is fusiform, with numerous narrow varices, the canal being open and slightly bent to one side. The genus is Tertiary and Recent.

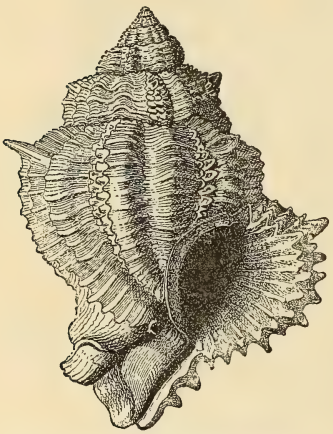


Fig. 708.—*Murex Sedgwickii*. Miocene. (After Zittel.)

Family 46. Volutidæ.—In this family the shell is turreted or convolute, with a shining, often enamelled, surface, and a large body-

whorl. The aperture is notched in front or produced into a short canal, and the columella is obliquely plaited. There is usually no operculum, the foot is very large, and the mantle is often reflected over the shell. The living members of the *Volutidæ* are chiefly inhabitants of warm seas, and are often remarkable for their brilliant colours. The family does not appear to have existed till towards the later portion of the Cretaceous period; but it is abundantly represented in the Tertiaries, and attains its maximum in existing seas. The most important genera are *Voluta*, *Volutomitra*, *Mitra*, and *Marginella*.

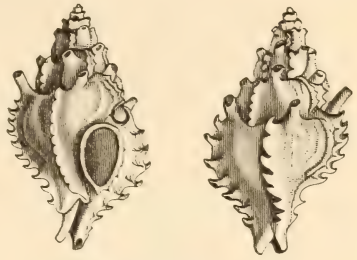


Fig. 709.—*Typhis tubifer*. Eocene Tertiary.

The true Volutes form the genus *Voluta* (fig. 710), characterised by the short spire, large, deeply-notched aperture, and columella with several plaits. A large number of recent, and still more numerous fossil, forms of *Voluta* are known, the earliest types appearing in the Cretaceous rocks. The genus has been divided into a number of sub-genera, one of the most important of which is *Volutilithes*, represented by numerous forms in the Cretaceous and older Tertiary deposits.

Mitra, *Volutomitra*, and *Turricula*, are hardly distinguishable as fossils, all of them possessing a spindle-shaped shell, with a long spire and a small aperture, an anterior notch or short canal being present, and the columella being obliquely plaited. The typical *Mitræ* have the outer lip thickened and smooth within, and are characteristic of the Tertiary and Recent periods. In *Turricula* the outer lip is striated internally, and the surface is transversely ribbed. Forms of this type range from the Cretaceous rocks to the present day. In *Volutomitra* (Tertiary and Recent) the outer lip is thin and simple.

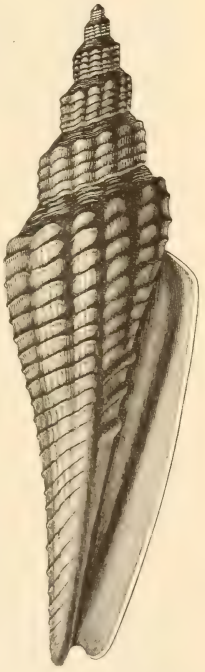


Fig. 710.—*Voluta elongata*. Chalk.

In *Marginella*, lastly, the shell is smooth, with a short or concealed spire; and the aperture is truncated

in front, with a wide notch, a plaited columella, and a thickened outer lip. The genus is Tertiary and Recent.

Family 47. Harpidæ.—The type of this family is the genus *Harpa*, in which the shell is ventricose, with a short spire and a large body-whorl; the whorls are convex and adorned with transverse ribs, and the aperture is large and notched in front. The genus comprises marine types, and is confined to the Tertiary and Recent periods.

Family 48. Olividæ.—In this family the shell is elongated and solid, with a narrow aperture, a sharp smooth outer lip, and a callous columellar lip. The members of this family are marine, and are essentially inhabitants of warm seas.

The "Olives" (*Oliva*) and "Rice-shells" (*Olivella*) are characterised by their cylindrical polished shell (fig. 711, A), with a short spire, a long narrow aperture, notched in front, and an obliquely striated columella. The living Olives are tropical and subtropical in their distribution. A single species of *Olivella* has been detected in the Cretaceous rocks of California, but with this exception, the Olives are wholly Tertiary and Recent. The genus *Ancillaria* (fig. 711, B) is nearly related to *Oliva*, but the spire is produced, and is covered with shining enamel. Species of *Ancillaria* occur in the Upper Cretaceous rocks, but the genus is mainly Tertiary and Recent.

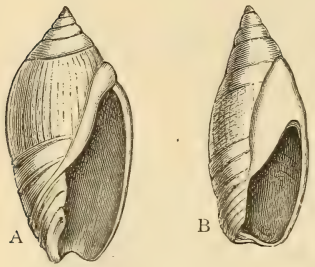


Fig. 711.—A, *Oliva Branderi*, Eocene; B, *Ancillaria glandina*, Eocene.

Family 49. Cancellariidæ.—The type of this family is the genus *Cancellaria*, in which the shell is oval or turreted, with a large body-whorl; and the aperture notched or canaliculated in front. The columella is obliquely plaited, and the surface is cancellated. The genus ranges from the Chalk to the present day.

Family 50. Conidæ.—In this family the shell is inversely conical, with a very short spire and an elongated body-whorl. The aperture is long and narrow, notched in front, the columellar lip not plaited, and the outer lip smooth and often notched at or near the suture. The members of this family are all marine, and they are principally Tertiary and Recent, the oldest types being Cretaceous.

The principal genus of this family is *Conus* itself, using this name in a comprehensive sense. The "Cones" are distinguished by their short spire and regularly conical shell (fig. 712). Very numerous recent species of *Conus* are known, and also a consider-

able number of fossil forms, the earliest representatives of the genus appearing in the Middle Cretaceous rocks. The genus *Conorbis*, of the Eocene and Oligocene, nearly resembles *Conus*, but the spire is elevated and pointed, the shell thus becoming biconical.

Family 51. Pleurotomidæ.—In this family the shell (fig. 713) is spindle-shaped, with an elevated spire and an elongated aperture, produced in front into a straight canal. The outer lip has

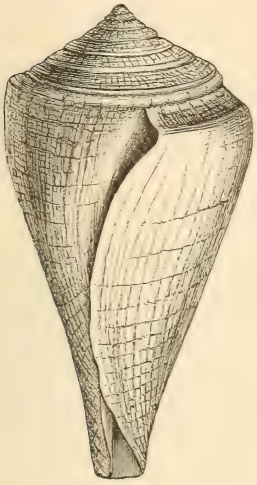


Fig. 712.—*Conus deperditus.* Eocene.

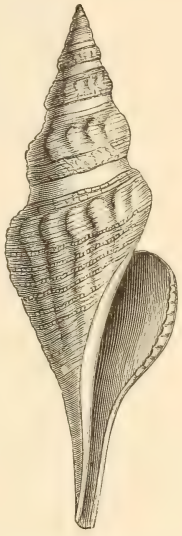


Fig. 713.—*Pleurotoma rostrata.* Eocene.

a slit or sinus posteriorly, near the suture. The principal, or sole, genus comprised in this family is *Pleurotoma* itself, which attained an enormous development in the Tertiary period, and is still very largely represented. A few forms of *Pleurotoma* are known to occur in the Cretaceous rocks; but, according to Zittel, more than nine hundred Tertiary species are known, while over six hundred and fifty recent species exist. The genus *Pleurotoma* has been divided by conchologists into a number of subordinate groups, which are sometimes regarded as subgenera, sometimes as independent genera.

Family 52. Terebridæ.—This family comprises only the genus *Terebra*, in which the shell is many-whorled and turreted, and the body-whorl is of small size. The aperture is small, and there is a short canal or notch in front; while the outer lip is thin and sharp. The living species of *Terebra* inhabit warm seas; and the oldest fossil forms appear in the Eocene Tertiary.

CHAPTER XXXIX.

DIVISIONS OF GASTROPODA—continued.

BRANCHIOGASTROPODA—*continued.*

Order II. Opisthobranchiata.

The Opisthobranchiate Gastropods are distinguished by the fact that the branchiæ are situated behind the heart, and the auricle is behind the ventricle of the heart. The gills are not usually contained in a special branchial chamber, and are commonly more or less exposed to view. The shell is wanting or present, being in the latter case often rudimentary. The sexes are united in the same individual.

The *Opisthobranchiata*, or "Sea-slugs," may be divided into two sections, the *Tectibranchiata* and *Nudibranchiata*, according as the branchiæ are protected or are uncovered. In the Nudibranchiate forms, the branchiæ, when differentiated, are placed externally on the back or sides of the body, and the animal, in the adult condition, is destitute of a shell. Owing to their want of hard structures, no traces of the Nudibranchs have ever been detected in the fossil condition. On the other hand, in the Tectibranchiate forms, the mantle more or less extensively covers the gills, and very generally secretes a shell, which may be so greatly developed as to entirely enclose the animal when withdrawn within it. Owing to their possession of a shell, the majority of the families of the Tectibranchs are known to occur in the fossil state, the earliest forms appearing in the Carboniferous rocks. The number of fossil Tectibranchiates is, however, very limited as compared with that of the Prosobranchiate Gastropods, the following four families being those which have yielded fossil representatives :—

Family 1. Actæonidæ (Tornatellidæ). — In this family the shell is spiral or convoluted; the aperture is long and narrow, rounded or sometimes channelled in front; and the columella is

generally plaited. The living examples of this family are mostly small and thin-shelled, but some of the fossil forms are of considerable size and are thick-shelled. The family attains its maximum in the Secondary period.

In the genus *Actæon* (*Tornatella*) the shell is ovate, with a well-marked spire, the outer lip thin, and the columella with one or more strong folds. The genus ranges from the Trias to the present day. In *Actæonina*, ranging from the Carboniferous Limestone to the present day, the shell is elongated, and the columellar lip is without folds. In *Actæonella* the shell is ventricose, with a very large body-whorl, and the columella shows three strong oblique folds in front. This genus is characteristic of the Middle and Upper Cretaceous deposits, having a remarkably wide range in space, and being sometimes represented by very numerous individuals in particular zones.

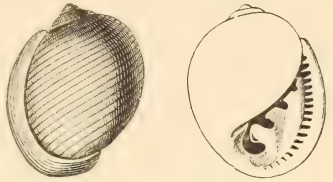


Fig. 714.—*Cinulia avellana.* Chalk.

In the genus *Cinulia* (fig. 714) the shell is globular, with a small spire; the outer lip is reflected and crenulated interiorly; and the columella exhibits toothlike folds. The genus is exclusively confined to the Cretaceous rocks. In *Cylindrites*, again, the shell is cylindrical, and smooth, with an elongated aperture and a fold on the columella. The genus ranges from the Trias to the Cretaceous rocks.

Lastly, the genus *Ringicula* (fig. 715) is now usually placed in this family. The shell in this genus is ventricose, with a small spire, the columella callous and deeply plaited, and the outer lip thickened and reflected. The earliest forms of *Ringicula* appear in the Cretaceous rocks, but the genus attains its maximum in the later Tertiaries and at the present day.

Fig. 715.—*Ringicula ventricosa.* Pliocene. (After Searles Wood.)

Family 2. Bullidæ.—In this family the shell is convoluted and thin, with a sharp outer lip and an elongated aperture. The spire is small or concealed, and the shell is often more or less completely invested by the soft parts of the animal. A large number of fossil forms of this family, beginning in the Trias, are known, and the group has attained its maximum at the present day. The three principal genera are *Bulla*, *Scaphander*, and *Cylichna*.

Fig. 716.—*Bulla suprajurensis.* Middle Oolites.

The genus *Bulla* (fig. 716) comprises the so-called "Bubble-

shells," in which the shell is ventricose, with a very large body-whorl and a deeply sunk spire. The fossil types are principally found in the Tertiary deposits. The Recent and Tertiary genus *Scaphander* is closely related to *Bulla*. Lastly, in *Cylichna* the shell is solid, and cylindrical in form, with a narrow aperture and a thickened columella. The species of this genus are numerous, and range from the Trias to the present day.

Family 3. Aplysiadæ.—In this family there is a thin horny shell, which is concealed by the reflection of the mantle over the back and sides of the animal. Two fossil species of *Aplysia* are stated to occur in the Pliocene deposits of Sicily.

Family 4. Pleurobranchidæ.—In this family the shell is limpet-like, or concealed, or may be wanting. The genus *Umbrella* appears to be represented in the Pliocene deposits, and dubious Secondary forms of the same have also been described.

Order III. Heteropoda.

The Gastropods included in the order of the *Heteropoda* or *Nucleobranchiata* differ from the typical members of the class in being *organised to lead an existence in the open ocean, locomotion being effected by a fin-like tail, or by a fan-shaped vertically-flattened ventral fin.* They are found swimming at or near the surface of the ocean ; and the body may be completely protected by a shell, within which the animal can retire, and which can be closed by an oper-

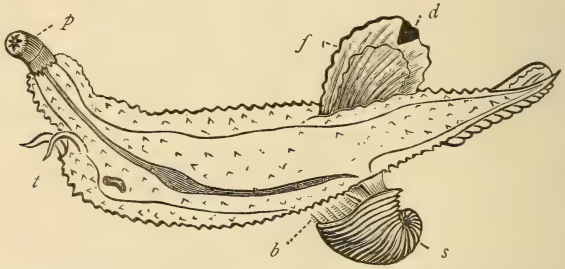


Fig. 717.—Heteropoda. *Carinaria cymbium*. *p*, Proboscis ; *t*, Tentacles ; *b*, Branchiæ ; *s*, Shell ; *f*, Foot ; *d*, Disc. (After Woodward.)

culum. In other cases, as in *Carinaria* (fig. 717), the body is large, and there is only a small shell protecting the gills and heart. In other cases, again, the shell is completely wanting. The order is divided into the two families of the *Firolidæ* and *Atlantidæ*, both of which comprise transparent delicate animals, which are either wholly naked or possess a shell of extreme tenuity and fragility.

The members of the *Firolidæ* are either shell-less, or possess a small hyaline shell, placed on the back, protecting the gills. The only member of this family which is known to be certainly represented in the fossil state is the existing genus *Carinaria* (fig. 717), a single species of which has been found in deposits of Miocene age.

In the *Atlantidæ* the animal is furnished with a well-developed but fragile shell, completely enclosing the body. In *Atlanta* itself the shell is rolled into a flat spiral, and the body-whorl is keeled, and exhibits a dorsal slit at the aperture, thus resembling the shell of the *Bellerophontidæ*. A single species of *Atlanta* has been found in the Tertiary deposits of San Domingo. Owing to the close resemblance of the shell of *Bellerophon* and its allies in external form to that of *Atlanta*, the former have been commonly regarded as Heteropods. The comparative thickness and solidity of the shell of the *Bellerophontidæ*, however, and the common association of the forms of this family with fossils of an unquestionable shallow-water type, forbid the reference of these singular Palæozoic Gastropods to the present order.

Order IV. Pteropoda.

The Pteropods or "Winged Snails" are pelagic Molluscs, found swimming near the surface in the open sea, the living forms being all of small size. They have no distinctly differentiated head, and the mouth is placed anteriorly in the centre of the fore-part of the foot, which is rudimentary. The lateral parts of the foot ("epipodia") are, however, developed into a pair of wing-like fins (fig. 718), by means of which the animal swims actively. The posterior part of the foot ("metapodium") is rudimentary, but in some cases may develop an operculum. In some groups (*Gymnosomata*) the mantle is rudimentary, and the adult is not provided with a shell. In other groups (*Thecosomata*) the mantle is well developed, and secretes a shell. In both sections of the order the embryo is furnished with a shell, but the larval shell is soon lost in the *Gymnosomata*; whereas in the great majority of the *Thecosomata*, the adult develops a secondary and permanent shell, of which the embryonic shell usually forms the initial portion. The shell of the *Thecosomata* generally is calcareous in composition, and in all the living forms is very delicate in texture. The so-called

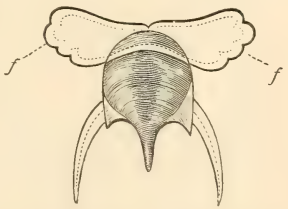


Fig. 718.—*Cavolinia* (*Hyalæa*) *tridentata*, showing the shell, and the lateral fins attached to the sides of the head (*ff*).

"shell" of *Cymbulia* is of a cartilaginous consistence, but it does not correspond with the shell of the other Thecosomatous Pteropods in its nature or origin. In the majority of the shell-bearing Pteropods the shell is symmetrical, but in the *Limacinidæ* it is coiled into a spiral. The Pteropods are all hermaphrodite, and the young pass through a metamorphosis.

The *Pteropoda* have been very generally regarded as a distinct class of the *Mollusca;* but the most recent investigations, more especially those of Dr Pelseneer, prove that in the essential details of their organisation they do not differ materially from the *Gastropoda*, of which class they should be considered as a division or order. The Pteropods fall naturally into the two sections of the *Gymnosomata* and the *Thecosomata*, the former devoid of any shell in the adult condition, while the latter (with the exception of the aberrant genus *Cymbulia*) possess an external calcareous shell. Owing to their having no hard parts capable of preservation in the fossil condition, the Gymnosomatous Pteropods have left behind them no traces of their past existence, and therefore require no further consideration here. On the other hand, the Thecosomatous Pteropods are known to occur as fossils, though opinions differ as to the true nature of many of the organisms which have been referred here.

As regards their *distribution in time*, the Tertiary rocks have yielded the remains of indubitable Pteropods, which differ in no respects from existing forms, and are, in fact, largely referable to existing genera. The whole series of the Secondary rocks has, on the other hand, yielded no remains of organisms which can be asserted to be unequivocal Pteropods. It is not, indeed, till we reach the Devonian and Silurian deposits that we meet with fossils which in all essential respects agree with the living Pteropods, and which appear to belong to such existing genera as *Styliola* (*Creseis*). It is true that these ancient representatives of *Styliola* have had their claim to be regarded as Pteropods strongly disputed, but it will be pointed out hereafter that there is at present no sufficient ground for denying their Pteropodal nature. The case, however, is different with the three remarkable groups of fossils typified respectively by the genera *Tentaculites*, *Hyolithes*, and *Conularia*, the age of which is exclusively or mainly Palæozoic. These ancient types differ in many respects from the typical Pteropods, and their true nature and position must be regarded in the meanwhile as more or less open to question. If these aberrant and problematical genera be provisionally included among the Thecosomatous Pteropods, the following are the principal families included in this division of the order :—

Family 1. Limacinidæ.—In this family the shell is twisted into

a left-handed spiral, and a spiral operculum is present. The anus is on the right side, and the pallial cavity is dorsal in position. It is not certain that any fossil forms of this family have been detected, but some minute shells from the Eocene, Miocene, and Pliocene deposits have been referred with considerable probability to the existing genus *Limacina* (*Spirialis*).

Family 2. Cavoliniidæ.—In this family the shell is bilaterally symmetrical and is not rolled up into a spiral. The anus is on the left side, and the pallial cavity is ventral. The shell has a variable form, but is essentially a hollow cone, which may be flattened dorso-ventrally or may be circular in section. The initial portion of the shell is generally distinct from the rest, and represents the larval shell (Pelseneer).

The types which have been described under the names *Creseis*, *Hyalocylix*, *Clio* (*sensu restricto*), and *Styliola*, are included by Dr Pelseneer under the common generic name of *Clio* (= *Cleodora*). In all these forms the shell (fig. 722, c) is a conical tube, sometimes circular in outline, sometimes oval, sometimes laterally keeled, the apex of the shell being pointed, or exhibiting a bulbiform enlargement due to the presence of a distinctly defined embryonic shell. Unquestionable remains of this group of Pteropods are found in the Miocene and Pliocene deposits.

In the Silurian and Devonian rocks of both the Old and New Worlds there occur minute conical calcareous tubes, which have been generally referred to *Styliola* or *Creseis*. As the type of these may be taken *Styliola* (*Creseis*) *fissurella* of the Devonian rocks of North America. In this remarkable form (fig. 719) the shell is a very delicate calcareous tube, of a conical form, circular in section, and without internal partitions, either longitudinal or transverse, the average length of the tubes being from one to three millimetres. The apex of the tube is commonly slightly bulbous (fig. 719, a), and is thus marked off as an "initial chamber" from the rest of the shell. The surface is without annulations, and may be smooth, or marked by fine transverse striæ, sometimes with longitudinal striæ as well (fig. 719, b). *Styliola fissurella* is exceedingly abundant in parts of the Devonian rocks of North America, and sometimes gives rise by the accumulation of its shells to thin bands of limestone (fig. 720), which may have a considerable geographical range. Dr Pelseneer

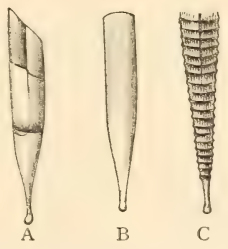


Fig. 719.—a and b, Specimens of *Styliola* (*Creseis*) *fissurella*, Hall, from the Devonian rocks (Hamilton Group) of North America, enlarged about six times, showing the embryonic shell at the apex; c, Apical portion of the tube of *Tentaculites gracilistriatus*, from the same formation, enlarged to show the embryonic shell. (After Hall.)

denies that the so-called "Styliolæ" of the Silurian and Devonian rocks can be referred to the *Pteropoda* on the grounds of their great size, the absence of an embryonic shell, and the fact that no existing species of *Clio* has the shell longitudinally striated. The first two of these objections, however, do not apply to *Styliola fissurella* and its allies, since the tube is smaller than that of some of the existing species of *Clio*, and an embryonic shell is present; while the third objection would appear to be of anything but a conclusive character. It is certainly remarkable that, admitting the Pteropodal nature of *Styliola fissurella*, no traces of forms of the same genus should have hitherto been met with in the later Palæozoic and in the Secondary deposits, and that the genus is not known to be again represented till the Miocene period is reached. Palæontology, however, is rich in examples of gaps of this kind, and little importance can be attached to a seeming hiatus, which may any day be partially filled up.

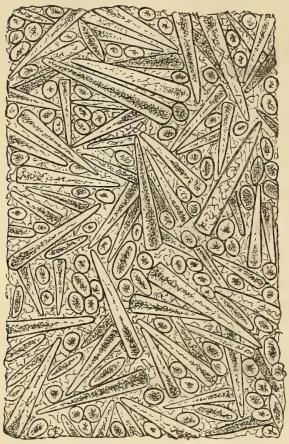


Fig. 720. — Thin section of limestone from the Devonian rocks of Canandaigua, North America, composed almost entirely of the tubes of *Styliola fissurella*, enlarged twenty times. (Original.)

Of the remaining genera of the *Cavoliniidæ*, *Cuvieria* has a straight conical shell, the hinder pointed half of which is generally caducous in the adult. The genus is represented by existing species and by late Tertiary types. Lastly, in *Cavolinia* (*Hyalæa*) the shell (fig. 721) is globular, the dorsal plate comparatively flat, and prolonged into a hood, the ventral plate bulging and convex, the aperture contracted, with a lateral slit on each side, and the hinder end with one to three spines. The genus is represented by Miocene and Pliocene forms as well as by existing species.

Fig. 721.—*Cavolinia* (*Hyalæa*) *Orbignyana*. Miocene Tertiary.

Family 3. Cymbuliidæ.—This family includes only the recent genus *Cymbulia*, which differs from all the other Thecosomatous Pteropods in the possession of a straight, bilaterally symmetrical, cartilaginous "pseudoconch," which is formed by the thickening of the integument, and is not homologous with the shell of the ordinary Pteropods. As the "shell" of *Cymbulia* is not capable of preserva-

tion in the fossil state, no record of the past existence of the genus can be obtained.

Family 4. Hyolithidæ.—With this family we enter upon the consideration of a series of remarkable Palæozoic fossils, which have been generally referred to the *Pteropoda*, though their true affinities cannot be considered as certainly established. The type of this family is the genus *Hyolithes* (= *Theca* and *Pugiunculus*), which has been generally regarded as allied to the recent *Clio* or *Styliola* (fig. 722, c), though the dimensions of the shell much exceed those of the ordinary species of the latter, and there are other differences as well. The shell (fig. 722, d, f, h) in *Hyolithes* is bayonet-shaped or conical, usually straight, but sometimes curved,

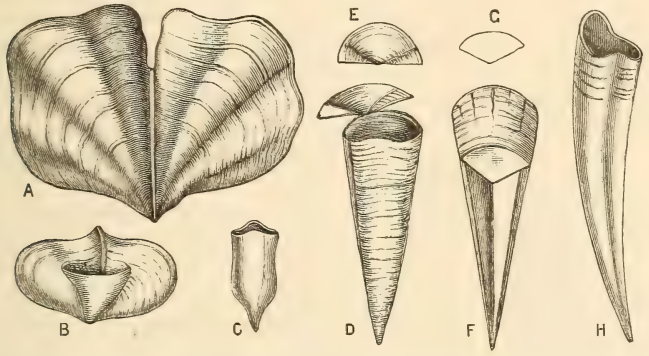


Fig. 722.—a, *Pterotheca corrugata*—Ordovician (after Salter); b, *Pterotheca transversa*—Ordovician (after Salter); c, *Styliola* (*Clio*) *depressa*—Miocene; d, *Hyolithes* (*Theca*) *operculatus;* and e, its operculum—Upper Cambrian (after Salter); f, *Hyolithes aratus*—Upper Cambrian; and g, Cross-section of the same (after Salter); h, *Hyolithes acutus*—Silurian (after Eichwald).

of thin texture, transversely striated or smooth, sometimes with marginal ribs, but without lateral appendages. The mouth of the shell is trigonal, and in some forms, at any rate, is provided with an operculum (fig. 722, e), or occasionally furnished with curved lateral appendages. The length of the shell varies, but is commonly from an inch to an inch and a half. The species of *Hyolithes* are most abundant in the Upper Cambrian and Ordovician rocks; but there are various Silurian and Devonian forms, and the genus is recorded as occurring in both the Carboniferous and the Permian rocks. *Pterotheca* (fig. 722, a and b), of the Ordovician, in many respects resembles *Hyolithes;* but the median dagger-shaped shell is bordered by lateral concentrically-striated expansions or alations, thus coming to superficially resemble the carapace of certain of the Phyllopods.

The Devonian genus *Coleoprion* has a cylindrical and conical

shell, the exterior of which is marked with chevron-shaped striæ. Possibly allied to the preceding types, but of wholly uncertain affinities, are the genera *Hemiceras* and *Salterella*. In the first of these are conical elongated shells, of circular section, in which the walls are thickened by the deposition of concentric calcareous lamellæ, till only a small tubular space is left in the centre. The genus is Ordovician. *Salterella*, of the Upper Cambrian and Ordovician rocks, comprises conical tubes, resembling the preceding in shape, but consisting of several hollow cones placed one within the other.

Family 5. Conulariidæ.—This family includes only the remarkable genus *Conularia* (fig. 723), the true relationships of which have not been clearly established, though the genus is usually placed among the *Pteropoda*. The shell in *Conularia* is very thin, and is pyramidal in shape, the transverse section being rhomboidal or four-sided. The apex is often deciduous, and the internal cavity may be partitioned off near the apex by one or more transverse plates. The aperture of the shell is contracted, and is partially closed by tongue-like prolongations from its corners. Each of the four faces of the shell may be provided along its entire length with an internal median longitudinal fold, sometimes with two such, but these may be wanting or rudimentary. Externally, each face of the shell is divided into two equal halves by a longitudinal groove, corresponding with the internal fold above mentioned; and the surface is ornamented with transverse, smooth, or tuberculated ridges, which are angulated in the middle line of each face, so as to form a series of obtuse angles, the apices of which point towards the aperture.

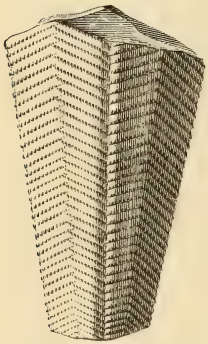


Fig. 723.—*Conularia ornata*. Devonian.

The genus *Conularia* attains its maximum in the Ordovician and Silurian rocks, some of these early types attaining a length of nearly a foot, with a breadth of more than an inch. The Devonian and Carboniferous rocks have yielded a few species, and two forms occur in the Permian, while a single species has been detected in the Trias, and another has been recorded from the Lias.

Family 6. Tentaculitidæ.—This family comprises only the genus *Tentaculites*, in which the shell (fig. 724) is comparatively thick and solid, and has the form of a straight, elongated, conical tube, from half a centimetre up to three centimetres in length, which tapers to a closed apex at one end, and expands towards the other to a circular aperture. The tube is always circular in outline, and

the apex is often partially filled up with a secondary calcareous deposit, or may be partitioned off by one or more curved transverse plates (fig. 725, A). The initial portion of the shell may be smooth and without annulations, and may be simply pointed. In other cases, the apex is distinctly bulbiform (fig. 719, C), its starting-point being a dilated chamber, which appears in no respect to differ from the "embryonic shell" of *Clio* and other Pteropods. The whole of the tube, except the initial portion, is annulated by abruptly elevated rings, which become more remote as the aperture is approached; and the surface between the annulations is marked by fine encircling striæ, sometimes accompanied by longitudinal striæ as well.

Fig. 724.—*Tentaculites ornatus*. Silurian.

As regards its minute structure, thin sections show that the tube of *Tentaculites* is composed of two distinct layers of a different nature (fig. 725, B and C). The outer layer is very dense, and is thickened at intervals so as to form the annulations which are so characteristic of the genus. The inner layer is composed of transparent calcite, traversed by parallel lamellæ of a dark colour, which are approximately parallel to the surface of the tube. Both layers

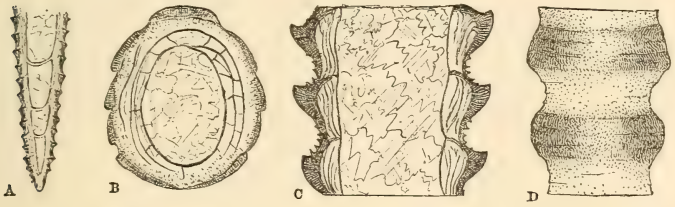


Fig. 725.—Minute structure of *Tentaculites attenuatus*, from the Devonian rocks (Hamilton Group) of Canada. A, Section of the apex of a tube, showing curved transverse partitions; B, Transverse section of the tube (the oval form of the tube is the result of pressure); C, Vertical section, taken through the middle of the tube; D, Vertical section traversing the wall of the tube, and showing its peculiar tubulated structure. The figures are enlarged about twenty times. (Original.)

are more or less extensively penetrated by a system of exceedingly minute tubuli (fig. 725, D), the direction of which is approximately at right angles to the surface.

The genus *Tentaculites* ranges from the Ordovician to the Devonian, occurring for the most part in limestones, and being often present in vast numbers in particular beds. In no case is the shell attached to any foreign body.

The affinities of *Tentaculites* cannot, in the present state of our knowledge, be determined with absolute certainty. The compara-

tive thickness and solidity of the shell, together with its remarkable minute structure, must be considered as points which militate against a reference of the genus to the Pteropods. On the other hand, its free habit of existence, its general form, its mode of occurrence, and its occasional possession of a distinct initial chamber or embryonic shell would support the view that it belongs to the *Pteropoda*. The occasional presence of curved internal septa is a point of small weight, one way or the other, since such transverse partitions are not absolutely unknown in recent Pteropods (*Cuvieria*). Still less stress can be laid upon the argument that *Tentaculites* can hardly be regarded as a Pteropod, seeing that the normal forms of the *Pteropoda* do not make their appearance till the Tertiary rocks are reached. Any weight that might be supposed to be carried by such an argument is counterbalanced by the fact that in *Styliola fissurella* and its allies we have Palæozoic forms which have not been shown to differ materially from existing types of Pteropods. By some palæontologists *Tentaculites* is regarded as belonging to the Tubicolar Annelides; and *casts* of the shell of *Tentaculites* are undoubtedly very similar to casts of the tube of *Cornulites*. The microscopic structure of the tube of *Tentaculites* is, however, widely different from that of *Cornulites*, while the tube shows no signs of having been at any time of life attached to any foreign body. It is, however, quite possible that *some* of the forms which have been referred to *Tentaculites* are really Annelidan in nature. Thus, Hall has pointed out that all the forms from the Ordovician rocks of North America which have been placed in *Tentaculites* are *curved* and are longitudinally striated; and he regards these, therefore, as probably truly belonging to *Cornulites* or to some related Annelidan genus.

Sub-Class II. Pulmogastropoda.

The Pulmonate Gastropods are essentially distinguished by the fact that the breathing-organ is a pulmonary chamber, formed by an inflection of the mantle, to which air is directly admitted by an external aperture; while the sexes are united in the same individual.

The most typical members of this division of Gastropods, such as the Land-snails and Slugs, are terrestrial in habit. Others, like the *Limnæidæ*, inhabit fresh waters, and either come to the surface to obtain air, or, in some cases, have the power of using the lung-chamber as an organ of aquatic respiration. A few forms only (*Siphonariidæ*, *Gadiniidæ*) are inhabitants of salt water.

The condition of the shell varies much, a few forms (*e.g.*, *Oncidium*) being wholly without a shell. In the Slugs, a shell is present, but is of small size, and is concealed within the mantle. In the ordinary Snails, again, and in the Pond-snails, there is a well-

developed external shell, within which the animal can entirely withdraw itself.

As regards their *distribution in time*, the completely shell-less forms are necessarily altogether unknown in the fossil condition, and the forms with a rudimentary and concealed shell are only known in the latest Tertiary deposits. The abundance of the ordinary shell-bearing forms as fossils depends mainly on the habits of the animal. As the preservation of an ancient land-surface in the crust of the earth is a matter of rare occurrence, the strictly terrestrial Pulmonates are not largely represented in the fossil state, their remains, in fact, occurring principally in lacustrine or fluviatile deposits intermingled with the shells of fresh-water types of Pulmonates. These latter are found in moderate numbers in fresh-water deposits of Secondary and Tertiary age. The oldest known types of the Pulmonate Gastropods have been found in the Carboniferous rocks.

The sub-class *Pulmogastropoda* may be divided into the two orders of the *Stylommatophora* and the *Basommatophora ;* but only a few of the more important families composing these can be noticed here.

Order I. Stylommatophora.

The Pulmonates included in this order have the eyes placed at the extremities of long feelers, which are retractile and capable of invagination. The shell may be rudimentary or even absent, but is usually well developed. The following are, from a palæontological point of view, the most important families included in this order :—

Family 1. Testacellidæ. — This family includes carnivorous Pulmonates, with a spiral shell of very variable size. In *Testacella* itself, the animal is slug-like, and there is a minute ear-shaped shell placed at the hinder end of the body. Fossil forms of this genus have been found in the later Tertiary deposits.

In *Glandina*, on the other hand, there is a well-developed spiral shell, within which the body of the animal can be withdrawn. The recent types of this genus inhabit warm regions, and the fossil forms date from the Upper Cretaceous period.

Family 2. Limacidæ.—In this family are comprised the "Slugs," in which there is a minute rudimentary shell concealed within the mantle. Species of *Limax* have been recognised as occurring in the late Tertiary and Quaternary deposits.

Family 3. Helicidæ.—This family includes the ordinary "Land-snails," in which there is a well-developed shell, capable of containing the entire animal. A large number of fossil representatives of this family are known, chiefly belonging to the Tertiary period, but

occurring also in deposits of Secondary age, and even in rocks as old as the Carboniferous formation. If *Dawsonella* be regarded as a member of the *Helicinidæ* (see p. 778), the oldest representatives of the *Helicidæ* are the *Zonites* (*Conulus*) *priscus* and the *Pupa* (*Dendropupa*) *vetusta* of the Coal-measures of North America, both of which were first discovered and described by Sir William Dawson.

In the genus *Helix* are the ordinary Land-snails, of which about two thousand living species are known, belonging to a large number of subgeneric groups. The shell in *Helix* is very variable in shape, sometimes conical, sometimes depressed, and sometimes discoidal; the aperture being transverse, crescentic or rounded in shape, and the columella being perforated or imperforate. The most ancient of the typical *Helices* appear in the Eocene rocks, and a large number of Tertiary species have been recognised.

In *Zonites* the shell is thin, usually hyaline, in the form of a

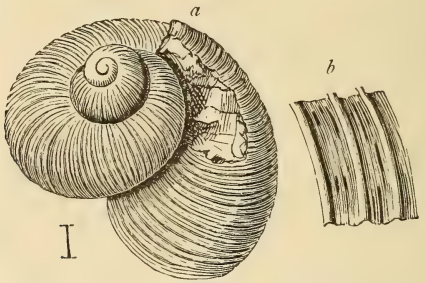


Fig. 726.—*Zonites* (*Conulus*) *priscus* (after Dawson). *a*, Specimen enlarged twelve diameters; *b*, Sculpture, magnified. Coal-measures, Nova Scotia.

depressed spiral, with a simple and sharp-edged peristome, and almost always umbilicated. The oldest example of this genus is the *Z. priscus* (fig. 726) of the Coal-measures of Nova Scotia. Other species occur in the later Tertiaries; and the *Archæozonites* of the Oligocene and Miocene deposits is nearly related to *Zonites*.

In *Bulimus* the shell is oval or turreted, the columella is straight, the aperture is oblong, and the outer lip is expanded and thickened. *Bulimulus* includes forms with a shell very similar to that of *Bulimus*, but with a generally thin lip and an elongated aperture. The earliest forms of *Bulimus* appear in the Upper Cretaceous rocks. In the genus *Achatina* the shell is like that of *Bulimus*, but the columella is twisted. No undoubted fossil representatives of this genus have been recognised.

In the genus *Clausilia* the shell is spindle-shaped, and is coiled into a left-handed spiral, the aperture being elliptical, and partially contracted by two folds of the inner lip. The mouth of the shell

is closed when the animal is withdrawn within it by a movable calcareous plate ("clausilium"). A large number of recent species of *Clausilia* are known, but the fossil forms are not numerous, and the oldest of them appear in the Eocene.

In the genus *Pupa* the shell is cylindrical or oblong, with a rounded, often toothed aperture and a reflected outer lip. The oldest known type of this genus is the *Pupa* (*Dendropupa*) *vetusta* of the Coal-measures of Nova Scotia, discovered by Sir William Dawson in the hollow trunk of an erect *Sigillaria*. The aperture in this form (fig. 727) is devoid of teeth. An allied type is the *Pupa vermilionensis* of the Coal-measures of the United States. With these exceptions, the fossil *Pupæ* are all of Tertiary age.

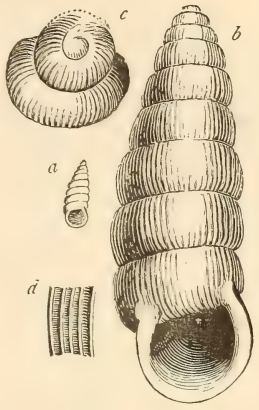


Fig. 727.—*Pupa* (*Dendropupa*) *vetusta* (after Dawson). *a*, Natural size; *b*, Enlarged; *c*, Apex enlarged; *d*, Sculpture, magnified. Coal-measures.

Lastly, in the genus *Succinea* the shell is thin and ovate, with a small spire and a large body-whorl, the aperture large and obliquely oval, and the outer lip thin. The "Amber-snails" live in moist places on land, and the known fossil species are confined to the Tertiary rocks. *S. oblonga* and *S. putris* are very common in the Loess.

Order II. Basommatophora.

In this order of Pulmonates the eyes are placed at the base of two feelers, which are contractile, but are not capable of invagination. Of the families of this order, the *Auriculidæ* and *Limnæidæ* are inhabitants of fresh waters, or are amphibious, or in other cases live in moist places on land, while the aberrant groups of the *Siphonariidæ* and *Gadiniidæ* are marine in habit.

Family 1. Auriculidæ.—In this family the shell is spiral, with a horny epidermis; the aperture is elongated, generally with a toothed outer lip; and the columella is folded. The members of this family inhabit salt-marshes and places overflowed by the sea. The principal genus is *Auricula* itself, which ranges from the Upper Jurassic rocks to the present day, but the fossil forms are of comparatively little importance.

Family 2. Limnæidæ.—In this family the shell is well developed, thin and horn-coloured, and of very variable shape. The aperture is simple, and the outer lip is sharp. The *Limnæidæ* are all in-

habitants of fresh water, and they are found in fluviatile and lacustrine deposits. They commence in the Jurassic period, members of this family having been described from the Lias (?) and from the Purbeck beds (Upper Jurassic). It is not, however, until we reach the base of the Cretaceous system (Weald Clay) that these forms appear in any abundance.

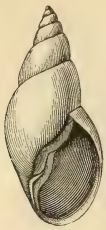


Fig. 728.—*Limnæa pyramidalis.* Eocene.

The genus *Limnæa* (fig. 728) includes the so-called "Pond-snails," characterised by their thin, spiral, elongated shells, with a large body-whorl and an obliquely-twisted columella. The species of this genus commence in the Upper Jurassic (Purbeck Beds), and they are abundantly represented in the Tertiary series.

In the genus *Physa* (fig. 729) the shell is left-handed ("sinistral"), ovate, thin, and polished, with the aperture rounded in front. Walcott has described a species of *Physa* as occurring in the Lower Carboniferous rocks of Nevada. With this exception, the oldest species of the genus occur in the Purbeck beds (Upper Jurassic) and Wealden (Lower Cretaceous). Most of the fossil species, however, belong to the Tertiary period, and the genus attains its maximum at the present day.

The genus *Planorbis* (fig. 730, A and B) comprises a number of well-known fresh-water shells, in which the shell is discoidal and

Fig. 729.—*Physa columnaris.* Eocene.

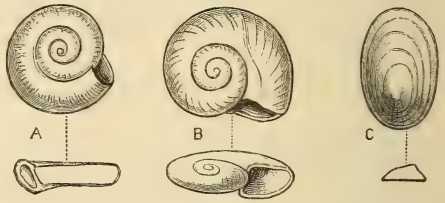


Fig. 730.—A, *Planorbis complanatus*, viewed from below and in front—Pliocene and Recent; B, *Planorbis discus*—Eocene—viewed from above and in front, reduced one-half; C, *Ancylus Matheroni*—Tertiary—viewed sideways and from above, the latter figure enlarged.

many-whorled, the aperture crescentic, and the lip thin. The fossil species of this genus date from the Lias (?), but are not plentiful except in the Tertiary deposits, from which numerous forms have been obtained.

Lastly, the genus *Ancylus* (fig. 730, C) comprises the so-called "River-limpets," distinguished by their thin limpet-shaped shell, the apex of which is approximated to the hinder margin. The fossil species are few in number, and the earliest forms appear in the Miocene deposits.

Family 3. Siphonariidæ.—This family comprises certain marine Gastropods, of amphibious habits, which agree with the normal Pulmonates in the possession of a pulmonary chamber. The shell is limpet-shaped, unsymmetrical, and usually radially ribbed. The muscular impression in the interior of the shell is interrupted by a lateral sinus corresponding with the opening of the pulmonary sac. The type-genus of this family is *Siphonaria* itself, the living species of which are found in tropical seas. The earliest fossil forms appear in the Eocene deposits, but the shell is with difficulty distinguished from that of the *Patellidæ*.

Family 4. Gadiniidæ.—This family comprises marine Pulmonates, which possess a patelliform shell, and differ from the preceding family only as regards the armature of the mouth. No undoubted fossil forms of the family are known, but Professor von Zittel is disposed to refer here the genus *Valenciennesia*, in which the shell is like that of a large limpet, but the apex is much incurved, and an internal sulcus and corresponding superficial fold extend from the apex to the right margin, and exist in a less developed form on the left side. This remarkable genus occurs in abundance in the brackish-water Upper Miocene deposits ("Congeria-beds") of south-eastern Europe.

CHAPTER XL.

POLYPLACOPHORA AND SCAPHOPODA.

Class III. Polyplacophora.

The class of the *Polyplacophora* comprises only the family of the *Chitonidæ*, which differs in many important respects from the Gastropods, and presents certain relationships with the Worms. The body in the *Chitonidæ* (fig. 731, A) is elongated and worm-like, bilaterally symmetrical, with the mouth at the anterior end, and the anus at the hinder extremity of the body. There is no differentiated head, nor are cephalic tentacles developed. The under surface of the foot forms a creeping disc; and the gills are numerous (fig. 731, *g*), and are contained in an imperfect pallial chamber or groove, between the margins of the foot and the edge of the mantle. The upper surface of the body is covered by the mantle, which secretes a "multivalve" shell (fig. 731, B), composed of eight transverse imbricated plates, which succeed one another from before backwards, and are embedded in the leathery or fibrous border of the mantle.

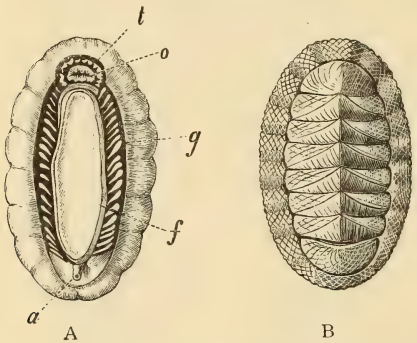


Fig. 731.—A, Under surface of a species of *Chiton* (after Cuvier): *t*, Fringe of tentacles round the mouth (*o*); *g*, Branchiæ; *f*, Under surface of foot; *a*, Anus. B, Shell of *Chiton squamosus*, reduced one-half. (After S. P. Woodward.)

The shell of the Chitons (fig. 731, B, and fig. 732) consists of eight valves placed in a line, the anterior or "cephalic" valve and the posterior or "anal" valve invariably differing from the six "intermediate" valves, which are similar to one another. Each of the intermediate valves is divisible by lines of sculpturing into a central

area (fig. 732, B, *m*) and two lateral areas (*l*). The upper or exposed surface of the valves is spoken of as the "tegmentum," while the "articulamentum" is a peripheral zone which supports and is partly covered by the tegmentum. The shell is entirely surrounded by, and more or less extensively embedded in, the "girdle" or "zona" formed by the border of the mantle, and variously covered on its upper surface with scales, spines, or bristles. The cephalic and the six intermediate plates have their apices at their posterior margin, but the apex of the anal plate is usually anterior.

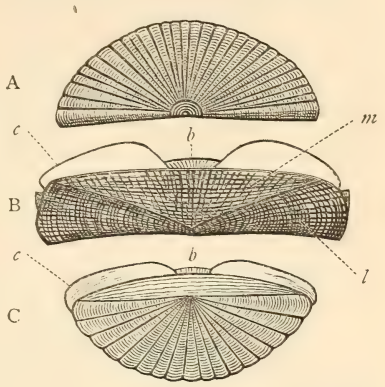


Fig. 732.—A, Cephalic valve, B, one of the intermediate valves, and C, anal valve of *Chiton magnificus*, viewed from the dorsal aspect: *m*, Central area of the valve; *l*, One of the lateral areas of the valve; *c c*, Apophyses or sutural laminæ; *b b*, Sinus and jugal area. (After Gray.)

The cephalic valve is usually semicircular in shape, and its front edge is generally prolonged into an "insertion-plate," or forward extension of the "articulamentum," by which it is embedded in the mantle. The intermediate valves are transverse in shape as a rule, and their front edges are furnished with forward extensions of the articulamentum, which serve to unite the successive valves, and are known as the "apophyses" or "sutural laminæ" (fig. 732, *c*). Posteriorly the intermediate plates usually possess "insertion-plates." The anal valve is variable in form and sculpturing, as well as in the position of its apex, but it has in front a pair of apophyses, separated by a median sinus (*b*), and it possesses an insertion-plate posteriorly. The insertion-plate of the anal valve may be similar in form to that of the cephalic valve, or may be different from it, and by this character the Chitons are grouped as "regular" or "irregular."

The tegmentum of the recent Chitons exhibits two sets of superficial circular apertures, one set large ("megalopores"), the other set of much smaller size ("micropores"). These apertures lead into corresponding sets of tubes, large and small, which perforate the shell vertically, and open below into a plexus of horizontal canals running in the space between the apposed surfaces of the tegmentum and articulamentum. These horizontal canals open internally, and lodge processes derived from the mantle, which send out ramifications into the canals connected with the "megalopores" and "micropores." These ramifications finally expand into differently-sized papilliform bodies ("megalæsthetes" and "micræsthetes"), which appear to be peculiar organs of touch. Further, as shown by Moseley, a number of the "megalæsthetes" are in some cases spe-

cially modified in structure, and become converted into minute eyes which are distributed over the exposed surface of the tegmentum.

The Chitons are inhabitants of the sea, and they are of rare occurrence as fossils, being more abundant in the Palæozoic than the Mesozoic or Kainozoic deposits. Under the name of *Holochiton*, Fischer has united the recent genus *Leptochiton* and a number of Palæozoic types which have been placed in groups under special names (*Helminthochiton*, *Gryphochiton*, &c.) The general characters of the "Holochitons" are the possession of an oval or elongated shell, in which the "insertion-plates" are obsolete or more or less developed, their margins being in the latter case entire, and showing neither fissures nor denticulations. Taken as a whole, the Palæozoic Chitons are characterised by the elongated form of the shell, the narrowness of the valves (fig. 733), the absence or rudimentary condition of the insertion-plates, and the widely separated sutural laminæ. In their narrow valves and elongated form the Palæozoic Chitons resemble the recent genus *Cryptoplax* (= *Chitonellus*), but the shell in the latter is formed wholly by the articulamentum, the valves are more or less separated, and the insertion-plates have fissured margins. As regards their geological distribution, the "Holochitons" range from the Ordovician to the Permian rocks, but the majority of the known forms are Carboniferous. Some of the Carboniferous types, however, possibly belong to *Cryptoplax* (*Chitonellus*). The conical calcareous plates of the Silurian rocks of Gotland, which have been described under the name of *Chelodes*, are regarded by Lindström as referable to the *Chitonidæ*. The plates of *Chelodes* show remarkable resemblances to those of the Chitons, but they are altogether peculiar in the fact that not only are there no insertion-plates, but the sutural laminæ are also wholly unrepresented.

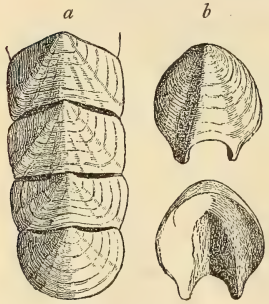


Fig. 733.—*Holochiton* (*Gryphochiton*) *priscus*, from the Carboniferous Limestone of Belgium. *a*, Four consecutive plates; *b*, Anal plate seen from the exterior and from the interior. (After De Koninck—copied from Zittel.)

But few representatives of the *Polyplacophora* have hitherto been found in the Secondary and Tertiary rocks, and these few appear to belong to the genus *Chiton* itself, in which the insertion-plates are well developed and possess fissured margins, those of the cephalic and anal valves being alike in form.

Class IV. Scaphopoda.

This class of Molluscs includes only the single family of the *Dentaliidæ*, the characters of which would assign to it a position in some respects intermediate between the Lamellibranchs and the Gastropods. The type of the group is the genus *Dentalium*, the animal of which is bilaterally symmetrical, and is enclosed in a continuous mantle, which secretes a tubular shell, which is open at both ends. From the large anterior aperture of the shell is protruded the foot, with a circle of tentacles surrounding the mouth, but there is no distinct head. The oral tentacles appear to discharge a respiratory function, but there are no specialised branchiæ, nor is a definite heart present. The nervous system is of the Molluscan type; the kidneys are paired; the sexes are distinct; and the pharynx is furnished with a radula.

The shell in the *Dentaliidæ* is in the form of a slightly curved calcareous tube (fig. 735), of conical form, but not spirally coiled. The shell is open at both ends, the anterior aperture being larger than the posterior, and the latter being sometimes simple, sometimes crenulated or fissured. The concave side of the tube corresponds with the dorsal side of the animal, and the ventral side is convex. No operculum is developed.

The *Dentaliidæ* are all marine, and live buried in sand or mud, with the wide anterior extremity of the shell downwards. The fossil forms begin at least as early as the Devonian, and some Ordovician and Silurian types have been recorded, though these are not free from doubt.

Fig. 734.—*Dentalium vulgare*, of the natural size, with the oral tentacles protruded from the anterior opening of the shell. (After Lacaze-Duthiers.)

Fig. 735.—*Dentalium Bouei*. Miocene. (After Deshayes.)

In the genus *Dentalium* (figs. 734 and 735) the tubular shell is smooth, or longitudinally striated, or annulated; the anterior aperture is simple and is not contracted; and the posterior aperture is typically truncated and entire. *Entalis* is hardly separable from *Dentalium* proper, but there is a short slit at the posterior aperture on the ventral (convex) side

of the tube. The fossil species of *Dentalium* may be confounded with the tubes of Tubicolar Annelides, or a reverse mistake to this may be made. Species of *Dentalium* have been described from the Ordovician rocks of Russia by Eichwald, but the nature of these is not absolutely certain. Undoubted forms of the genus appear in the Devonian rocks, and a number of Carboniferous species are known. In the Secondary and Tertiary rocks the genus is well represented, the later forms being usually more ornate as regards the characters of the surface than are the older types.

In the genus *Siphonodentalium* (*Gadus*) the tubular shell may or may not be contracted towards its anterior extremity, but is always attenuated behind ; and the posterior aperture is incised or lobulated. The surface is smooth or finely striated. The genus ranges from the Cretaceous rocks to the present day. Lastly, in the Recent and late Tertiary genus *Cadulus*, the tube is swollen in its middle, and both its apertures are entire, the hinder one being crenulated.

CHAPTER XLI.

CLASS V. CEPHALOPODA.

The members of the class *Cephalopoda* are *bilaterally symmetrical Molluscs, with a large head, and having the body enclosed in a muscular mantle. The fore-part of the foot is split up into eight or more muscular processes or "arms," which surround the mouth; while the epipodia are well developed, and give rise, by apposition or fusion, to a muscular tube ("funnel") through which the effete water of respiration is expelled. One or two pairs of gills are contained within the pallial sac, and the sexes are always distinct.*

The *Cephalopoda*, comprising the Cuttle-fishes, Pearly Nautilus, &c., constitute the most highly organised of the classes of the *Mollusca*. They are all marine and carnivorous, and are possessed of considerable locomotive powers. At the bottom of the sea they can walk about, head downwards, by means of the arms which surround the mouth, and which are usually provided with numerous suckers or "acetabula." They are also enabled to swim, partly by means of lateral expansions of the integument or fins (not always present), and partly by means of the forcible expulsion of water through the tubular "funnel," the reaction of which causes the animal to move in the opposite direction.

The body in the *Cephalopoda* is bilaterally symmetrical, the cephalic region being conspicuously marked out, and being separated from the visceral region, which is enclosed in the mantle (fig. 736). The head bears a pair of large globular eyes, and has the mouth placed in the centre of its anterior surface. The mouth is surrounded by a circle of long muscular processes or "arms," formed by the splitting up of the margins of the foot. In the Cuttle-fishes there are always either eight or ten "arms," and these are provided with muscular suckers, which can be used in prehension. In the Pearly Nautilus, on the other hand, the arms are numerous, and are not furnished with suckers. The lateral margins of the foot ("epipodia") are, again, either placed in

apposition (*Nautilus*) or are actually united (Cuttle-fishes), in such a manner as to form a muscular tube, known as the "funnel." The funnel (fig. 736, *f*) is placed on the lower surface of the body, with its anterior extremity projecting beyond the mantle, while it opens behind into the pallial chamber. It serves for the elimination of the water which has been used in respiration, and the out-going currents also carry away with them the excretions of the kidneys and of the ink-sac, together with the fæces. By the contractions of the mantle, the water contained in the pallial sac can also be driven through the funnel in a succession of jets, driving the animal backwards through the water.

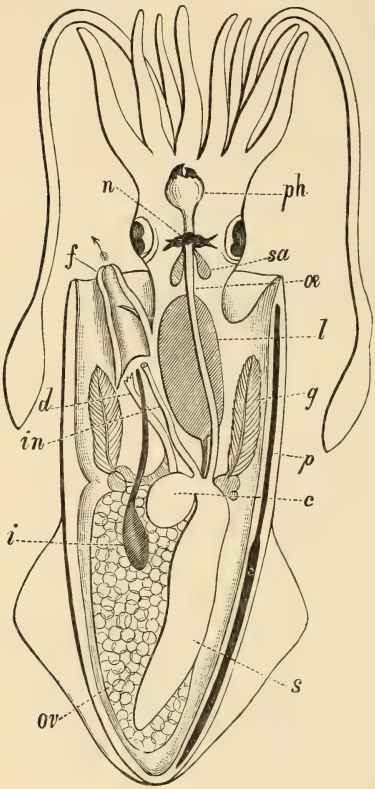


Fig. 736.—Diagram of the structure of a Cuttle-fish. *ph*, Pharynx, with the horny mandibles; *sa*, Salivary glands; *œ*, Œsophagus; *s*, Stomach; *c*, Gastric cæcum; *in*, Intestine; *l*, Liver; *n*, Œsophageal nerve-collar; *g*, One of the gills, with the branchial heart at its base; *i*, Ink-bag, its duct opening along with the intestine and generative duct at the base of the funnel; *ov*, Ovary; *d*, Oviduct (the nidamental and accessory glands are omitted); *f*, Funnel, *p*, Pen, lying in the mantle dorsally.

The mouth in the Cephalopods conducts into a powerful buccal cavity or pharynx (fig. 736, *ph*) containing two powerful mandibles, working vertically, resembling the beak of a parrot in shape, and either horny (as in the Cuttle-fishes), or partially calcified (as in *Nautilus*). There is also a toothed tongue or "radula." The intestine is short, and the anal opening is placed at the base of the funnel. The Cuttle-fishes possess a special glandular organ, the "ink-bag" (fig. 736, *i*), which secretes an inky fluid, which the animal can discharge into the water, so as to facilitate its escape when menaced or pursued. The duct of the ink-sac opens, along with the intestine, at the base of the funnel; but in the Pearly Nautilus and its extinct allies the ink-gland is entirely absent.

A well-developed heart is present in the Cephalopods, and the

respiratory organs are in the form of plume-like gills placed symmetrically on the sides of the body within the pallial sac. The Cuttle-fishes (Dibranchiate Cephalopods) have two gills, one on each side, while the Pearly Nautilus and its allies (Tetrabranchiate Cephalopods) have four gills, two on each side. The currents of water needed in respiration are maintained by the alternate contractions and expansions of the muscular walls of the mantle-sac. In each expansion the water finds its way into the pallial chamber by the opening between the rim of the mantle and the neck; and in each contraction it is expelled through the tube of the funnel, which is so constructed as to allow of the egress but to prevent the ingress of the water.

The nervous system of the *Cephalopoda* is highly developed, and its central masses form an œsophageal nerve-collar, which is protected by a cartilaginous plate.

The sexes are in different individuals, and the males and females are commonly more or less unlike externally, the former often having one of the arms specially modified to serve as an intromittent organ. The ducts of the generative glands open at the base of the funnel, and each individual, besides the essential organs of reproduction (testis or ovary), generally possesses accessory glands. The most important of these accessory glands in the females are known as the "nidamental glands," and they secrete a viscid material which unites the eggs together.

The *shell* of the *Cephalopoda* is sometimes external, sometimes internal. The internal skeleton (fig. 737) is known as the "cuttle-bone," "sepiostaire," or "pen" (*gladius*), and may be either corneous or calcareous. In some cases it is rendered complex by the addition of a chambered portion or "phragmacone," which is to be regarded as a visceral skeleton or "splanchnoskeleton." In *Spirula* (fig. 737, *c*) the phragmacone is the sole internal skeleton, and is coiled into a spiral, the coils of which lie in one plane, and are near one another, but not in contact. It thus resembles the shell of the Pearly Nautilus, but it is *internal*, and differs, therefore, in this respect from the *external* shell of the latter, though it is so far external that the last chamber lodges part of the viscera. The only living Cephalopods which are provided with an external shell are the Paper Nautilus (*Argonauta*) and the species of Pearly Nautilus (*Nautilus*); but not only is the structure of the animal different in each of these, but the nature of the shell itself is entirely different. The shell of the Argonaut is involuted, but is not divided into chambers, and it is secreted by the webbed extremities of the two dorsal arms of the female. The arms are bent backwards, so as to allow the animal to live in the shell, but there is in reality no organic connection between the shell and the body of the animal. In fact,

the shell of the Argonaut, being confined to the female, and serving by its empty apex as a receptacle for the ova, may be looked upon as a "nidamental shell," or, as it is secreted by a modified portion of the foot, it may more properly be regarded as a "pedal shell." The shell of the Pearly Nautilus, on the other hand, is a true pallial shell, and is secreted by the body of the animal, to which it is organically connected. It is involuted, but it differs from the shell of the Argonaut in being divided into a series of chambers by shelly

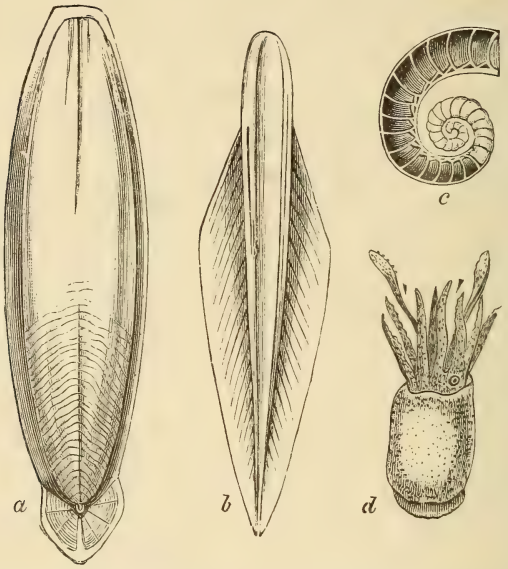


Fig. 737.—*a*, Internal skeleton of *Sepia ornata*; *b*, Pen of *Histioteuthis Bonelliana*; *c*, Shell ("phragmacone") of *Spirula fragilis*; *d*, Animal of *Spirula Peronii*.

partitions or septa, which are pierced by a tube or "siphuncle," the animal itself living in the last chamber only of the shell.

The *Cephalopoda* are divided into two extremely distinct and well-marked orders, termed the *Dibranchiata* and *Tetrabranchiata*, in accordance with the number of gills possessed by the animal. The former comprises all the true Cuttle-fishes; whilst the latter, though abundantly represented in past time, has no other living representatives than three or four species of the genus *Nautilus*.

As regards their *distribution in space*, the Cephalopods are exclusively inhabitants of the sea, and sometimes attain a great size. They live partly in the open sea and partly in shallow water close to shore, and are carnivorous in habit.

As regards their general *distribution in time*, the oldest forms of

the *Cephalopoda* (*Orthoceras* and *Cyrtoceras*) appear in the Upper Cambrian rocks. All the known Palæozoic representatives of the class belong to the order of the *Tetrabranchiata*, whereas the order of the *Dibranchiata* makes its first appearance in rocks of Triassic age. The Tetrabranchiates attain their maximum in the Secondary period, about six or seven thousand fossil forms being already known from strata of Palæozoic and Mesozoic age. On the other hand, but few Tertiary Tetrabranchiates have been recorded, and the order is represented at the present day by the single genus *Nautilus*. The order of the *Dibranchiata*, on the contrary, attains its maximum development at the present day.

CHAPTER XLII.

DIVISIONS OF THE CEPHALOPODA.

Order I. Tetrabranchiata.

The Tetrabranchiate Cephalopods are distinguished by the possession of *an external many-chambered shell, the last and largest chamber of which lodges the body of the animal. The chambers are separated by calcareous partitions or "septa," perforated by a membranous tube or "siphuncle." The head is furnished with numerous fleshy "tentacles," which are not provided with suckers; the branchiæ are four in number, two on each side of the body; the funnel does not form a complete tube; and there is no ink-bag.*

This order of the Cephalopods is represented at the present day by the single genus *Nautilus*, with four living species, and we may take the well-known Pearly Nautilus (*N. pompilius*) as the type of the division. The body of the Pearly Nautilus consists (fig. 738) of a posterior visceral mass and an anterior cephalic region, the whole being contained in the capacious outermost chamber (body-chamber) of the shell, from which the head can be protruded at will. The shell is rolled up into a flat spiral, and the position of the animal is such that the "funnel" (fig. 738, *f*) is turned towards the convex side of the shell, which is thus the ventral side, the concave side being dorsal. The visceral mass is included in the mantle, which is thin behind, but becomes thicker in front, being reflected on the dorsal side as a kind of collar over the convexity of the preceding whorl, which it invests with a black shelly deposit. The animal is attached to the shell by a double shell-muscle, while the posterior extremity gives off a membranous tube or "siphuncle," which pierces the successive septa centrally, and is continued backwards through the entire series of air-chambers.

The front portion of the "foot" surrounds the animal's mouth, and is furnished with a number of cylindrical, retractile "tentacles," which are not provided with suckers. Dorsally a portion of the

foot is thickened, and forms a fleshy fold or "hood" (fig. 738, *c*), which abuts against the preceding whorl of the shell. On the ventral side the median portion of the foot is converted into two muscular lobes, which are placed in apposition but are not fused with one another, thus forming the "funnel." As in all the Cephalopods, the funnel serves for the expulsion of the currents of water which have passed over the gills, as also for the escape of the undigested portions of the food and the generative products.

The mouth is placed in the centre of the head, and is armed with two horny mandibles, partially calcified towards their extremities, and shaped like the beak of a parrot, except that the inferior man-

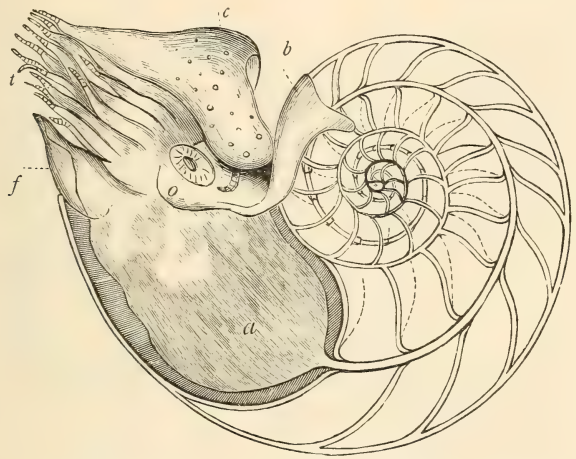


Fig. 738.—Pearly Nautilus (*Nautilus pompilius*). *a*, Mantle; *b*, Its dorsal fold; *c*, Hood; *o*, Eye; *t*, Tentacles; *f*, Funnel.

dible is the longest. A "radula" is present, and the intestine terminates at the base of the funnel. The heart is contained in a large viscero-pericardial sac (or "pericardium"), and consists of a ventricle, which receives four branchial veins; but there are no "branchial hearts." The branchiæ are contained within the mantle-cavity, and are four in number, two on each side. No ink-gland is developed. The sexes are distinct, and the reproductive organs of the female consist of an ovary, with two oviducts (the left rudimentary), and an accessory nidamental gland.

The only structures possessed by the Pearly Nautilus which are capable of preservation in the fossil condition are the mandibles and the shell, since the foot in this genus secretes no structure which can be compared with the "operculum" of the Gastropods. Leaving out of sight the "Aptychi" of the Ammonites, it is from fossil

beaks or shells that we derive our knowledge of the extinct Tetrabranchiates; and it is therefore necessary to study these parts in some detail, and with reference to the entire order.

In the living Pearly Nautilus the horny mandibles, which compose the "beak," are calcified towards their tips, the upper mandible more extensively so than the lower one. Similar beak-like jaws have been long known as occurring in the Secondary and Tertiary rocks, and they have been described under the name of *Rhyncholites*. The Jurassic and Cretaceous fossils included under the name of *Rhynchoteuthis* (fig. 739) are very similar to *Rhyncholites*, and are doubtless the calcified mandibles of some species of *Nautilus*, or of

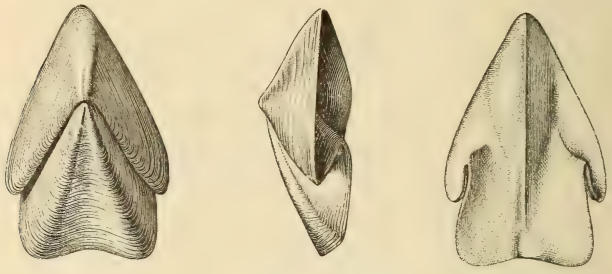


Fig. 739.—*Rhynchoteuthis Astierianus*. Lower Greensand (Cretaceous).

some allied type. In the Palæozoic rocks, in which the *Nautiloidea* are abundantly represented, the fossil beaks, except for a Carboniferous "Rhyncholite," are unknown.

The *shell* in all the Tetrabranchiates resembles that of the Nautilus in having a larger or smaller body-chamber, preceded by a chambered portion, which is divided into compartments by shelly partitions or "septa" (fig. 738). The chambers are usually spoken of as the "air-chambers," on the belief that they are filled with some gas secreted by the animal itself, but some authorities take the view that they are naturally filled with water. In all the Tetrabranchiates the chambers are traversed throughout by an originally membranous tube or "siphuncle," which is connected with the hinder end of the visceral sac.

In the Pearly Nautilus, as before pointed out, the animal is so related to its shell that the "funnel" is turned towards the convex side of the latter, the aperture of the shell showing a corresponding sinuation on that side. Hence, in the living Pearly Nautilus the convex side of the shell is ventral, and the shell is "exogastric." In various fossil Nautiloids, however, it can be shown that the shell-aperture is excavated on the inner or concave side, at which point we must suppose the "funnel" to have been placed. In such

"endogastric" types the concave side of the shell is the ventral side, the dorsal side being convex. In a great many fossil forms, however, there is no clear evidence as to the position of the animal in relation to its shell; and in such cases, as in the Ammonites, it is advisable to employ the terms "external" and "internal" for the convex and concave sides of the shell, since we do not know which side is "dorsal" or "ventral."

The shell of the Tetrabranchiates may be regarded as essentially a more or less elongated cone, the pointed end of which is parti-

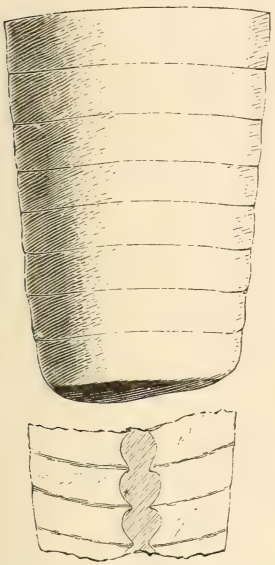


Fig. 740.—Fragment of *Actinoceras crebriseptum*—Cincinnati Group, North America, of the natural size. The lower figure is a section showing the air-chambers, and the form and position of the siphuncle. (After Billings.)

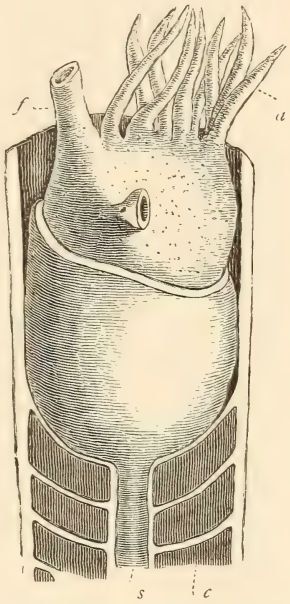


Fig. 741.—Restoration of *Orthoceras*, the shell being supposed to be divided vertically, and only its upper part being shown. *a*, Arms; *f*, Muscular tube ("funnel") by which water is expelled from the mantle-chamber; *c*, Air-chambers; *s*, Siphuncle.

tioned off into air-chambers, while the body-chamber is situated at the wide end (figs. 740 and 741). In some cases, as in *Orthoceras* and *Baculites*, the shell retains permanently its primitive form as a straight cone. In other cases the originally straight cone may be slightly bent (*Cyrtoceras*); twisted into a hook (*Hamites*); doubled on itself (*Ptychoceras*); or coiled into an open spiral, the turns of which may lie in one plane (*Gyroceras*) or may pass obliquely round an imaginary axis (*Helicoceras*). Very generally the volutions of the

shell are in contact with one another, in which case the coils may lie in one plane (*Nautilus*, *Ammonites*, &c.), or they may pass obliquely round an axis (*Turrilites*). In the discoidal types (such as Nautilus and the Ammonites) the last volution may more or less completely conceal the preceding turns of the spiral. In other cases the earlier coils of the shell remain visible, and the shell becomes umbilicated.

The surface of the shell in the Tetrabranchiates may be nearly smooth, or may show nothing more than delicate lines of growth. In other cases the surface may be more or less conspicuously adorned with various kinds of sculpturing, which may have a direction corresponding with the long axis of the shell, or may be at right angles to this. Thin sections show that the shell is composed of two principal layers, of a different nature. The outer layer forms a thin porcellanous stratum, which is lined throughout by a thicker nacreous layer, which alone forms the septa between the air-chambers.

The "septa," or partitions between the successive air-chambers, vary greatly in number in different types of the Tetrabranchiates.

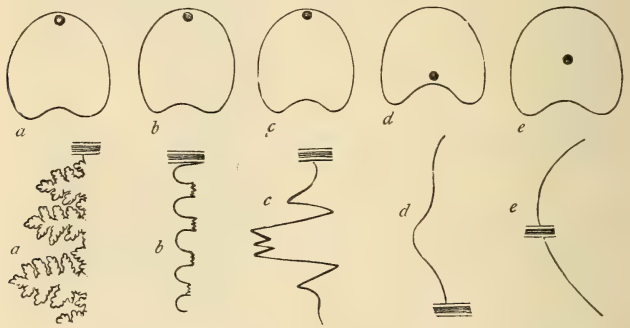


Fig. 742.—Diagram to illustrate the position of the siphuncle and the form of the septa in various Tetrabranchiate Cephalopods. The upper row of figures represents transverse sections of the shells, the lower row represents the edges of the septa. *a a*, *Ammonite* or *Baculite*; *b b*, *Ceratite*; *c c*, *Goniatite*; *d d*, *Clymenia*; *e e*, *Nautilus* or *Orthoceras*.

Whatever their number may be, they are usually placed in each individual at approximately uniform distances apart in each successive portion of the shell; but the last two or three septa are commonly closer to one another than the rest, probably in consequence of an impairment of the vitality of the animal with advancing age. Up to a certain period of the animal's life, new chambers are successively formed as the increasing size of the body necessitates the acquisition of more room, but the process by which the animal moves forwards prior to the development of a fresh septum is not perfectly understood. The edges of the septa, where they become

continuous with the shell-wall, are known as the "sutures," and the form of these necessarily varies with that of the septa themselves. In one great division of the Tetrabranchiates (viz., the *Nautiloidea*) the septa are simply curved or slightly lobed, and the "sutures" are more or less completely plain. In the other great division of the order (viz., the *Ammonoidea*) the septa are folded and complex, and the "sutures" are angulated, zigzag, lobed or foliaceous (fig. 742). The form of the "sutures" cannot be determined from the exterior, so long as the shell is preserved; but in fossil forms, in which the shell itself is commonly more or less extensively removed, the form of the sutures can be readily studied, and affords characters of high morphological value.

The "siphuncle" in the Tetrabranchiate Cephalopods has the form of a tube connected in front with the hinder end of the body, and continued backwards throughout the entire series of air-chambers. The precise function of the siphuncle is uncertain, but it probably serves to maintain the vitality of the shell. In the Pearly Nautilus the siphuncle is a membranous tube, the walls of which are to some extent strengthened by the deposition of calcareous granules. In some fossil Tetrabranchiates these calcareous deposits are so extensively developed that the wall of the siphuncle may become completely calcified. The proper sheath of the siphuncle, formed in this way, must, however, be carefully distinguished from certain other calcareous envelopes which may come to more or less completely enclose the siphuncular tube. Thus, in the Pearly Nautilus each septum is prolonged backwards at the point where it is perforated by the siphuncle as a short shelly tube — "neck" or "funnel" — which encloses the anterior portion of each segment of the siphuncle. In some Tetrabranchiates these "septal necks" do not merely form short collars round the siphuncle, but each is continued backwards from the septum in which it originates to the septum next behind (fig. 743, *si*); so that the proper siphuncle becomes enclosed in a complete secondary investment. In the majority of the Nautiloids the septal necks are directed, as in the Pearly Nautilus, *backwards* from each septum, and such forms are said to be "retrosiphonate." On the other hand, the majority of the

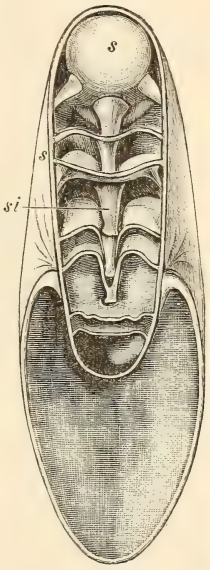


Fig. 743.—Partial section of the shell of *Aturia aturi*, showing the "septal necks" (*si*). From the Miocene deposits of Dax, Bordeaux.

Ammonoid Tetrabranchiates have the septal necks continued *forwards* from the producing septa, and are therefore said to be "prosiphonate." In many of the extinct types of the *Nautiloidea* the internal structure of the siphuncle is highly remarkable, the cavity of the tube often becoming contracted by organic deposits of secondary origin; but the structures in question will be more fully considered later on. Lastly, important distinctions are drawn in the Tetrabranchiates from the position of the siphuncle in relation to the shell. In the *Ammonoidea* the siphuncle is always marginal, and is mostly placed on the external side of the shell. In the *Nautiloidea*, on the other hand, the siphuncle may pierce the septa centrally (as in the Pearly Nautilus); or it may be subcentral; or in other cases it may be marginal, being then sometimes external, sometimes internal in position (fig. 742).

The development of the shell of the Pearly Nautilus is, unfortunately, unknown; but it has been shown that there are important distinctions in the form and structure of the initial chamber of the

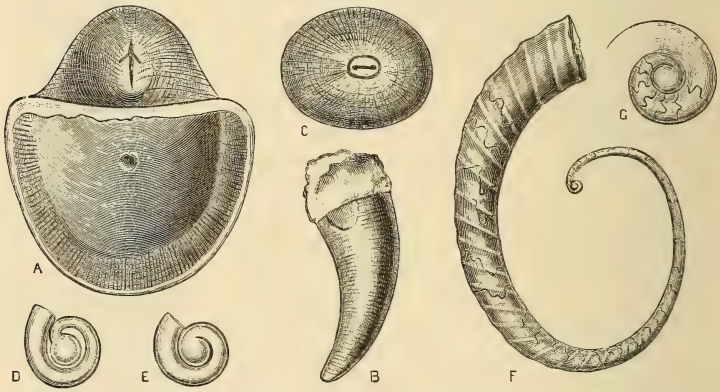


Fig. 744.—Development of Tetrabranchiate Cephalopods. A, The inner end of the shell of *Nautilus pompilius*, enlarged, showing the initial chamber and the cicatrix; B, *Cyrtoceras præposterum*—Silurian, showing the commencement of the shell; and (C) the initial chamber viewed from below, showing the cicatrix; D, Inner portion of the shell of *Goniatites bicanaliculatus*—Devonian, showing the inflated protoconch; E, First turn of the spire of *Goniatites sublamellosus*—Devonian; F, *Crioceras Studeri*—Cretaceous, enlarged, showing the protoconch; G, Protoconch and first turn of the spire of *Ammonites quadrisulcatus*—Cretaceous, enlarged. (After Barrande.)

shell in the two groups of the *Nautiloidea* and *Ammonoidea* respectively. In the Ammonoids the initial chamber of the shell (fig. 744, D—G) constitutes an inflated, spheroidal, oval, or pyriform sac, the so-called "protoconch" (or "ovisac"), which corresponds with the "nucleus" of the shell of the Gastropods, and is separated by a constriction from the first air-chamber. The siphuncle commences as a closed and dilated tube, which deeply indents the front wall of

the protoconch, but does not penetrate into the cavity of the latter. Munier-Chalmas has shown, further, that the cavity of the protoconch is traversed by a tubular organ or "prosiphon," which abuts against the front wall of the chamber, but does not communicate with the proper siphuncle, the place of which it is supposed to take in early life. In the *Nautiloidea*, on the other hand, the initial chamber of the shell (fig. 744, A, B, C) is a simple cone, which is not constricted off from the first air-chamber and is not inflated. The initial element of the siphuncle is a somewhat dilated cæcal tube, which indents the front wall of the initial chamber, but does not enter its cavity. The external surface of the initial chamber is usually marked by a network of transverse and longitudinal striæ, which mostly become obsolete in the adult shell. The hinder extremity of the initial chamber also exhibits an oval, rounded, or slit-like scar or cicatrix (fig. 744, A and C). The presence of this cicatrix would seem to show, as held by Hyatt, that the initial chamber of the Nautiloids does not correspond with the "protoconch" of the Ammonoids; and it seems not improbable that there existed in the former a deciduous protoconch, which is now represented only by a small vacuity in the centre of the shell (in the spirally-inrolled types). Hyatt, indeed, has described and figured the remains of this protoconch as occurring in certain species of *Orthoceras*. On this view, the initial chamber of the shell of the Nautiloids is really the first air-chamber, and the cicatrix in its posterior wall marks the point where this communicated with the caducous protoconch.

The order of the *Tetrabranchiata* may be divided into the two sub-orders of the *Nautiloidea* and *Ammonoidea*, typified respectively by the Nautili and the Ammonites. The *Ammonoidea* are regarded by Fischer as a separate order of the *Cephalopoda;* while the characters of the protoconch are regarded by some as affording ground for a reference of this division to the Dibranchiates rather than to the Tetrabranchiates.

Regarded as a whole, the Tetrabranchiate Cephalopods form a group which early attained its maximum, and is now almost extinct. The Palæozoic Tetrabranchiates are in the main of a decidedly simpler type than those which followed them. The largest number of generic types existed during the Mesozoic period, and the forms of this epoch are morphologically the most complex. With the close of the Secondary period disappeared almost all the characteristic Mesozoic types, and the order was left without any representative in the Tertiary rocks except the simple and ancient genus *Nautilus* and its immediate allies. As regards the two great sections of the order, the *Nautiloidea* are the most ancient, dating their existence from the Upper Cambrian. Not only is this the case, but they are pre-

eminently Palæozoic, only a few generic types surviving into the Secondary period. On the other hand, the *Ammonoidea* are pre-eminently Mesozoic in their range, being represented in the Palæozoic deposits earlier than the Carboniferous only by such comparatively simple types as *Clymenia* and *Goniatites*. With but limited and local exceptions, the *Ammonoidea* are not known to have survived into even the commencement of the Kainozoic period; and all the living *Tetrabranchiates* belong to the single genus *Nautilus*.

Sub-Order I. Nautiloidea.

In this division of the *Tetrabranchiata* the shell is straight or bent, or variously coiled, the aperture being simple or contracted, and the ventral side being commonly indicated by an emargination of the apertural edge. The sutures are simple, rarely undulated or denticulate; and the septa are concave towards the shell-aperture. The siphuncle is variable in position, and its cavity is often contracted by internal deposits. The "septal necks" are usually short, though sometimes long, and are generally directed backwards, the shell being "retrosiphonate." The initial chamber is conical, and has a cicatrix.

This sub-order includes the genus *Nautilus*, and a large number of wholly extinct types. The general characters of the shell have already been spoken of in dealing with the *Tetrabranchiata* as a whole; but there are a few special points which may be shortly noticed here.

The *aperture* of the body-chamber in the Nautiloids is variably shaped. In some cases, as in *Orthoceras*, the aperture is simple, as it is in the Pearly Nautilus; but the lateral margins of the aperture may be prolonged forwards, so that a sinus is produced on the convex and concave sides of the shell. The most marked and constant of these sinuses may be assumed to correspond with the funnel, and therefore to represent the ventral side of the animal; and, as previously pointed out, this is in *Nautilus* the convex side of the shell. While the aperture in many Nautiloids is simple, it becomes in other cases contracted by the bending inwards of the lateral prolongations of the mouth, so as to be converted into a dorsal and ventral opening connected by an intervening passage. In some cases the dorsal and ventral margins as well as the lateral ones are bent inwards, in which case the aperture (fig. 745) assumes a T-shaped

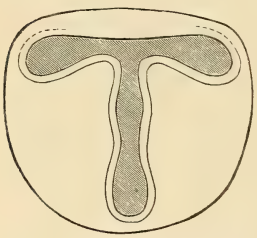


Fig. 745.—Aperture of the shell of *Gomphoceras Bohemicum*, reduced in size. (After Barrande.)

or key-hole-like character. According to the views of Barrande, the broad transverse part of the aperture represents in such cases the position of the head, while the rounded extremity of the vertical portion of the aperture corresponds with the funnel. It is clear, however, that with an aperture so contracted, the animal must have been incapable of protruding the head, as the living Pearly Nautilus can.

The dorsal and ventral aspects of the animal have no constant relation to the concave and convex sides of the shell among the *Nautiloidea*. In the Pearly Nautilus the convex side is the ventral one, but even within the limits of the same genus it is usual to meet with forms having the convex side ventral associated with others in which the concave side is ventral.

The *position of the siphuncle* is by no means constant among the Nautiloids, and bears no fixed relation to the aspects of the body of the animal, though it is commonly placed towards the ventral side. The siphuncle is upon the whole, however, most generally situated centrally or subcentrally, and when removed towards the margin it is usually external in the curved shells, though it may be internal. As regards its *structure* the siphuncle of the Nautiloids is, to begin with, a simple membranous tube, but it may become complex in process of growth. In many cases the cavity of the siphuncle becomes contracted by the formation in its interior of annular deposits of calcareous tissue (fig. 746, *or*), which were termed by Barrande "obstruction-rings"; and these may be so extensively developed as to completely obstruct the tube.

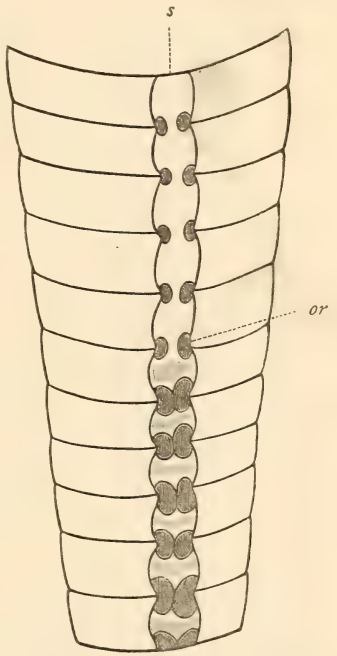


Fig. 746.—Vertical section of *Orthoceras angulatum*, Silurian, showing the siphuncle (*s*) contracted by the development of "obstruction-rings" (*or*) opposite the septa. (After Foord.)

The "*septal necks*" of the Nautiloids are almost always directed backwards, the shell thus being "retrosiphonate" (fig. 743). In the two genera *Nothoceras* and *Bathmoceras* alone are the septal necks turned forwards, so that the shell is "prosiphonate." In many forms, as in the existing Pearly Nautilus, the septal necks are short; but in other cases

they extend from septum to septum, and they may even fit into one another like so many funnels (as in the genus *Endoceras*).

Lastly, the "*sutures*," or the lines formed by the intersection of the septa with the surface of the shell, are simply curved, sigmoidally bent, or in some cases undulated. In a few cases short external and internal bendings of the suture ("lobes") may be developed, but these never constitute a conspicuous feature.

As regards their *distribution in time*, the earliest types of the *Nautiloidea* appear in the Upper Cambrian deposits, in which the genera *Orthoceras* and *Cyrtoceras* are represented. In the Ordovician rocks an enormous number of Nautiloids are known to occur, no less than four hundred and sixty-three species having been recorded by Barrande from rocks of this age in Bohemia alone. The maximum development of the group takes place, however, in the Silurian period, the Bohemian area having yielded to the researches of Barrande over a thousand species from deposits belonging to this system. In the later Palæozoic rocks the Nautiloids exhibit a progressive diminution in numbers, and only the genera *Nautilus* and *Orthoceras* survive the close of this epoch, the latter finally dying out in the Trias. The few known Tertiary types belong to *Nautilus* or to closely allied forms, and the sole existing representatives of the sub-order are four living species of *Nautilus*.

The sub-order *Nautiloidea* may be divided into the following families (see Foord's "Catalogue of the Fossil Cephalopoda in the British Museum"):—

Family 1. Orthoceratidæ.—In this family the shell is straight or slightly curved, the aperture is simple, and the siphuncle is usually slender and cylindrical. This family comprises the single genus *Orthoceras* (figs. 747, 748), in which the shell is in the form of a conical tube which is usually straight, but may be slightly curved. The aperture of the shell is not contracted, and the body-chamber is of large size. The septa are concave, usually horizontal, and generally far apart; and the siphuncle is usually slender and cylindrical, and may be central, subcentral, or excentric in position. The numerous species of *Orthoceras* are divided by Barrande into two principal sections—the Short-coned and Long-coned forms—according as the shell has the form of a short cone with a large apical angle, or of a prolonged cone with a small apical angle. The first of these groups is a very small one, and almost all the more common *Orthocerata* belong to the second section. Though the shell is typically straight, it may be gently curved throughout (as in *O. angulatum*); or it may be slightly bent towards the point of the cone, but otherwise straight (as in *O. unguis*). In the smaller forms, the initial chamber, with its cicatrix, is sometimes preserved.

The oldest known species of *Orthoceras* appears in the Upper

Cambrian (Upper Tremadoc beds of Wales), and very numerous forms of the genus have been recorded from the Ordovician rocks. The genus attains its maximum in the Silurian, more than five hundred species having been described by Barrande from rocks of this age in Bohemia. In the Devonian and Carboniferous rocks a great reduction in the number of species takes place ; a few Permian

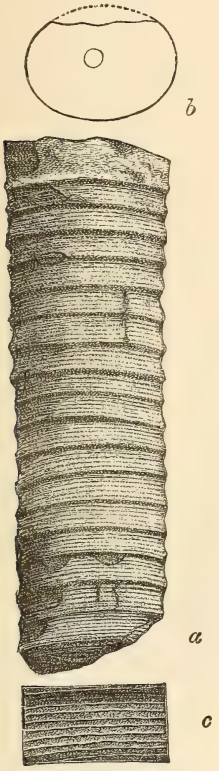


Fig. 747.—*a*, A broken specimen of *Orthoceras ornatum*, of the natural size, from the Silurian rocks of Gotland ; *b*, Transverse section of the shell, showing the position of the siphuncle ; *c*, Portion of the surface, enlarged. (After Foord.)

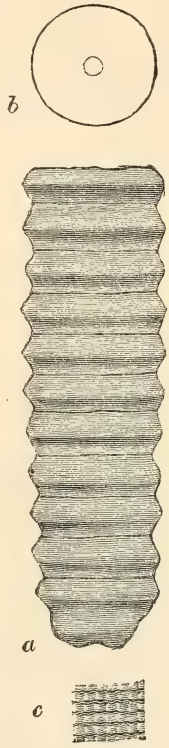


Fig. 748.—*a*, Cast of the shell of *Orthoceras Hisingeri*, from the Silurian rocks of Gotland, of the natural size ; *b*, Transverse section of the shell, showing the siphuncle ; *c*, Portion of the surface, enlarged. (After Foord.)

types are known ; and the last representatives of the genus are found in the Alpine Trias.

Family 2. Endoceratidæ.—In this family the shell is straight or slightly curved ; the siphuncle is marginal or sub-marginal, of large size ; and the septal necks are invaginated so as to form a wide tube within which the siphuncle is contained.

The type-genus of this family is *Endoceras*, in which the shell is straight and resembles that of *Orthoceras* in form. The septal necks (fig. 749, *sp*) are prolonged backwards to such an extent that each becomes inserted into the mouth of the neck of the septum next behind, thus forming a complete and wide tube which encloses the siphuncle. This siphuncular tube is marginal or sub-marginal, and may attain a diameter of one-half of that of the shell. The siphuncular tube is provided internally with a series of funnel-shaped sheaths (fig. 749, *sh*), which are not very numerous, and occur at irregular intervals. These were termed by Hall "embryo-sheaths," upon the belief that they were connected with reproduction; but

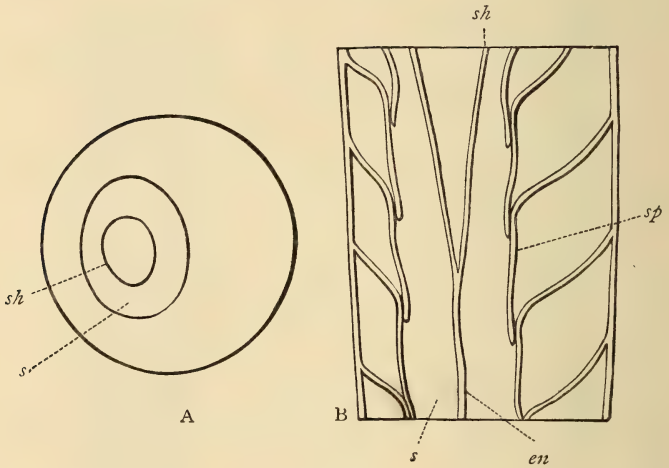


Fig. 749.—A, Transverse section of the shell of *Endoceras*; B, Vertical section of part of the shell of *Endoceras Wahlenbergi*, from the Ordovician rocks of Sweden (after Foord): *s*, Cavity of the siphuncle; *sp*, One of the "septal necks"; *sh*, One of the siphuncular sheaths; *en*, Endosiphon.

their true nature is not absolutely certain. In well-preserved examples, the great siphuncular space contains in its interior a cylindrical slender tube or "endosiphon" (fig. 749, B, *en*), which probably represents the calcified wall of the proper siphuncle. With the doubtful exception of one Silurian species (*E. ? Ommaneyi*) the genus *Endoceras* is confined to the Ordovician rocks. *Endoceras Wahlenbergi* (the *E. duplex* of many writers) is abundant in the Ordovician deposits of Scandinavia and Russia, and sometimes attains a length of six feet or more. Casts of the great siphuncular tube are not uncommon, and have the form of cylinders marked with oblique annulations.

In the genus *Piloceras* the shell is more or less broadly conical,

slightly curved, with a large marginal siphuncular tube, formed by the prolongation and conjunction of the septal necks, and provided internally with one or more funnel-shaped sheaths, which are united at the top with its margin. "These sheaths apparently communicated with one another by means of the endosiphon, which passed from the initial chamber into the siphuncular cavity by means of a large foramen, situated on the inner curvature of the siphuncle a little above the apical point" (Foord). The species of *Piloceras* are confined to the summit of the Cambrian and the base of the Ordovician deposits (the Durness Limestone of Britain and the Calciferous formation and Quebec group of North America).

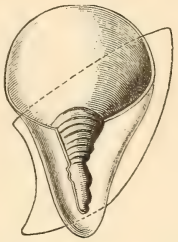


Fig. 750.—*Cyrtocerina typica*, Ordovician (Quebec Group), Canada. (After Billings.)

The genus *Cyrtocerina* (fig. 750), of the Lower Ordovician rocks (Quebec Group) of Canada, is perhaps allied to *Piloceras*. In this type, the shell is broadly conical and is curved, and there exists on the concave side of the shell a wide marginal siphuncular tube.

Family 3. Actinoceratidæ.—In this family the shell is straight or slightly curved, and the siphuncle is of large size and is composed

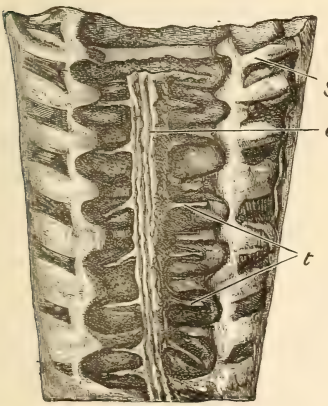


Fig. 751.—Weathered fragment of *Actinoceras Bigsbyi*, of the natural size, from the Ordovician rocks of Lake Huron. *s*, Septa; *en*, Endosiphon, with some of its tubuli (*t*). (After Foord.)

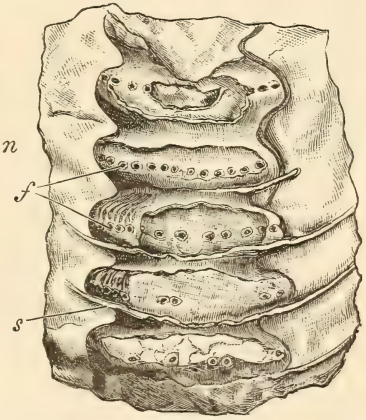


Fig. 752.—Fragment of *Actinoceras Bigsbyi*, from the Ordovician rocks of Kentucky, of the natural size. *s*, One of the septa; *f*, Foramina in the siphuncle by which the tubuli thrown out by the endosiphon may have communicated with the septal chambers. (After Foord.)

of nummuloid segments or discs, its internal cavity being more or less extensively contracted by the development of "obstruction-rings."

The type of this family is the genus *Actinoceras* (figs. 751 and 752), in which the shell is elongate-conical, and often of large size. The siphuncle is very large, its diameter sometimes equalling half that of the shell; and it is greatly inflated between the septa, so that it comes to present a series of segments of a compressed-globular form. In the centre of the main siphuncular tube is a cylindrical "endosiphon" (fig. 751, *en*), and the space between this and the wall of the former is largely occupied by secondary calcareous deposits ("obstruction-rings") developed at the "necks" of the septa. "The endosiphon is provided with a distinct wall, and gives off at regular intervals between the septa a number of radiating canals or tubuli (fig. 751, *t*), which apparently penetrate the shelly covering or wall of the siphuncle" (Foord). The foramina by which these tubuli open externally form a ring round each segment of the siphuncle (fig. 752, *f*), and they may perhaps have served to transmit blood-vessels to the lining-membrane of the air-chambers. The genus *Actinoceras* ranges from the base of the Ordovician (Upper Cambrian?) to the Carboniferous limestone, the *A. giganteum* of this latter formation attaining a length of from four to six feet.

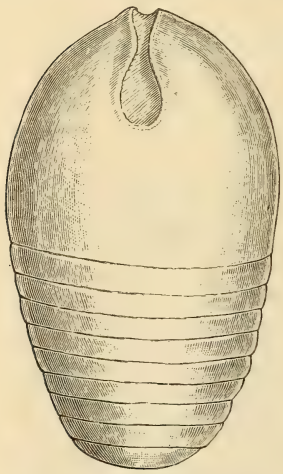


Fig. 753.—*Gomphoceras Bohemicum*, Silurian, Bohemia. (After Barrande.)

Allied to *Actinoceras* are the genera *Discosorus*, *Huronia*, and *Sactoceras*, all of which are confined to the Silurian rocks.

Family 4. Gomphoceratidæ. — In this family the shell may be approximately straight or more or less extensively curved, and the aperture of the shell is contracted and T-shaped (fig. 745). The principal genus in this family is *Gomphoceras*, with which may be included the forms usually spoken of as *Phragmoceras*.

In the most typical forms of *Gomphoceras* (fig. 753) the shell is approximately straight, or is very slightly curved, and the ventral side is always more convex than the dorsal, the shell being thus "exogastric"; while the siphuncle is situated towards the convex or ventral aspect. The aperture of the shell (fig. 745) is T-shaped; and the transverse orifice, corresponding with the head, may be widely expanded or may be contracted in the middle. The siphuncle is commonly subcentral, the septa are simply curved, and the body-chamber is of large size. The name of *Phragmoceras* has been given to forms of *Gomphoceras* in

which the shell (fig. 754) is more or less curved, the dorsal side being convex and the ventral side concave, and the shell being thus "endogastric;" while the siphuncle runs on the ventral aspect. The form of the aperture is not affected by this reversal of the curvature of the shell, except that the smaller opening of the T-shaped mouth, corresponding with the funnel of the animal, is now turned towards the concave side of the shell.

The genus *Gomphoceras* (including *Phragmoceras*) has been stated to range from the Ordovician to the Carboniferous; but, according to Foord, the pre-Silurian and post-Silurian types referred to this genus are of doubtful affinities, or are certainly known to be refer-

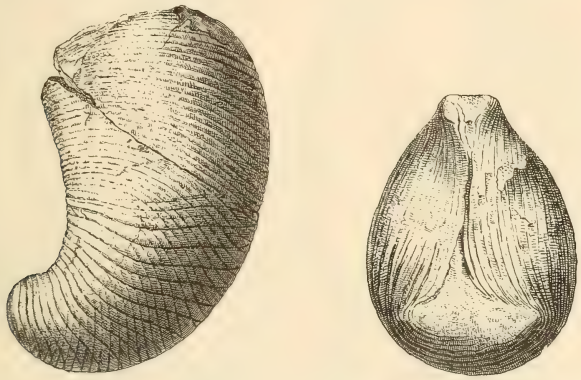


Fig. 754.—*Gomphoceras* (*Phragmoceras*) *ventricosum*. Silurian. The right-hand figure shows the form of the aperture.

able to other genera. The genus is therefore restricted, so far as clearly ascertained, to the Silurian period.

Family 5. Ascoceratidæ.—In this family the shell, when fully grown, is sac-like and truncated below, the body-chamber occupying most of the ventral side, while the last few septa are specially modified. The aperture may be simple or contracted.

The type of this family is the genus *Ascoceras* (fig. 755), which is defined by Foord as follows: "The shell is of a sac-like form, essentially straight, but always more convex on the ventral than on the dorsal side. The apex is unknown, the shell being always truncated. The transverse section may be elliptical or circular. The body-chamber occupies nearly the whole length of the shell on the ventral side, and contracts into a neck-like prolongation towards the aperture, which is simple. The last few septa are abnormal; they have the usual shape and position on the ventral side of the shell, but on the dorsal side they coalesce, and sweeping upwards in a sigmoid curve (as seen in section, fig. 755, *a*) form a series of

vaulted chambers, convex towards the aperture, and encroaching considerably upon the body-chamber. This extraordinary conformation of the septa on the dorsal side was doubtless caused by the shrinking of the animal in its shell on that side; whereby a cavity was created between the shell-wall and the mollusc, and then partitioned off in the manner above described. The short siphuncle is submarginal and near the ventral or convex border of the shell; it diminishes rapidly in size towards the body-chamber. The test is

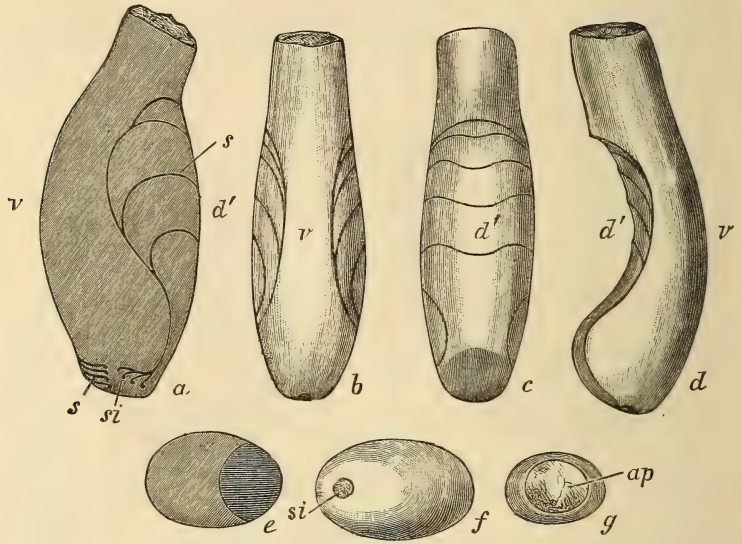


Fig. 755.—*Ascoceras Bohemicum*, Silurian, Bohemia. *a*, Longitudinal section, showing the septa (*s s*) and siphuncle (*si*); *b*, Ventral aspect of the cast of the shell, showing the reduction in size of the body-chamber caused by the encroachment of the septa; *c*, Dorsal view of the same specimen; *d*, Body-chamber, without the air-chambers; *e*, Transverse section taken in the centre of the fossil; *f*, Truncated posterior extremity, showing the position of the siphuncle (*si*); *g*, Anterior extremity, showing the simple form of the aperture (*ap*). The letters *v* and *d'* indicate the ventral and dorsal sides respectively. (After Barrande.)

relatively thick considering the size of the shell; its ornaments may consist of transverse lines or of annulations."

By the researches of Lindström it has recently been proved that *Ascoceras* begins in the form of an *Orthoceras*, having a cylindrical shell, with remote, simply curved septa, and a slender tubular siphuncle, and that the sac-like shell above described is only the final portion of the structure. When the organism has attained its full growth, and has formed the inflated *Ascoceras*-shell, the older, Orthoceratoid portion becomes decollated or cast off. It is, therefore, a matter of extreme rarity to find a complete specimen of *Ascoceras*, exhibiting both the older and later portions of the shell.

The species of *Ascoceras* are found in the Silurian rocks in Europe, and in the Ordovician rocks in North America. The Silurian genus *Glossoceras* resembles *Ascoceras* in general structure, but the aperture is contracted and lobed. The name of *Aphragmites*, again, is given to forms in which the peculiar arched septa at the side of the body-chamber are absent, the shell otherwise resembling *Ascoceras*.

Family 6. Poterioceratidæ.—The principal genus included in this family is *Poterioceras*, in which the shell is fusiform in shape, inflated in the central portion of its length, contracted towards the aperture, and very slender in its apical portion. The siphuncle is subcentral or marginal, and is inflated between the septa. The shell has a general resemblance to *Gomphoceras*, but the aperture is simple. The species of *Poterioceras* range from the Ordovician to the Carboniferous.

Family 7. Cyrtoceratidæ.—This family includes only the genus *Cyrtoceras*, in which the shell (fig. 756) is more or less curved, but

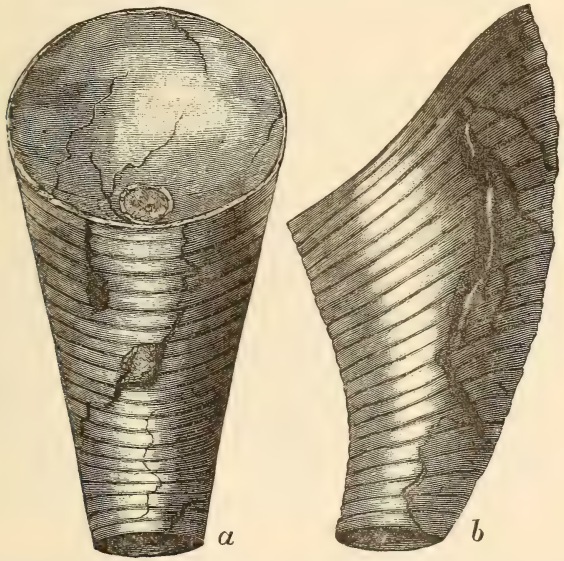


Fig. 756.—*Cyrtoceras obliquum*, Middle Devonian, Germany, about two-thirds of the natural size. *a*, Front view; *b*, Side view. (After Foord.)

does not form a complete volution, and the body-chamber is of large size. The septa are simple, concave forwards, and the siphuncle may be internal, external, or subcentral in position, and may be cylindrical or beaded. The shell is conical, or sometimes subcylindrical in form, some species being of the "brevicone" type, while others are "longicone." The genus *Cyrtoceras* ranges from

the Cambrian to the Carboniferous, and attains its maximum in the Silurian period, more than three hundred species having been described by Barrande from the Silurian deposits of Bohemia alone.

Family 8. Lituitidæ.—The shell (fig. 757) in this family has its earlier portion coiled into a flat spiral, while the later portion, including the whole or the greater part of the body-chamber, is produced in a straight line. The volutions of the spiral part of the shell may or may not be in contact, and the siphuncle is subcentral or internal. The septa are simple and concave, and the surface is transversely striated or ribbed.

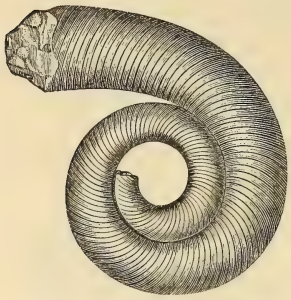


Fig. 757.—*Lituites cornu-arietis.* Ordovician.

In *Lituites* itself the uncoiled portion of the shell is very long, and the aperture is contracted, with a deep ventral sinus. The genus is found in the Ordovician and Silurian rocks. The Silurian genus *Ophidioceras* resembles *Lituites* in most respects, but the disjunct portion of the shell is short, and contains a portion only of the body-chamber. Lastly, in the genus *Discoceras*, also from the Silurian, the terminal and produced portion of the shell is short, but the aperture differs from that of *Ophidioceras* in being simple.

Family 9. Trochoceratidæ.—In this family the shell is rolled up into a spiral, the coils of which do not lie in a single plane. In *Trochoceras* the shell is unsymmetrically coiled, and the last volution may be partially disjunct. The septa are concave, and the siphuncle is usually placed between the centre and the convex external margin; while the aperture is simple. The genus ranges from the Ordovician to the Devonian, but the great majority of the species are Silurian. The Silurian *Adelphoceras* differs from *Trochoceras* in having a contracted aperture to the shell.

Family 10. Nautilidæ.—In this family the shell is spirally inrolled, the coils lying in one plane, and the aperture being simple or contracted. Of the numerous generic types included in this family, the following are the most important:—

In the Ordovician genus *Trocholites* the shell is discoidal and umbilicated, and the septa are concave, the suture-lines being simple or feebly lobed. The siphuncle is sub-marginal, placed towards the internal side, and the septal "necks" are long, and reach from one septum to the next.

In *Gyroceras* (fig. 758) the shell is in the form of a flat spiral, the coils of which are not in contact with one another. The aperture is simple, with a ventral and dorsal sinus; the sutures are simple;

the siphuncle is variable in position, but is usually placed between the centre and the convex side; and the surface is commonly adorned with tubercles or ribs. The genus ranges from the Silurian to the Carboniferous.

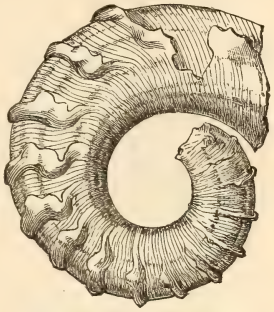


Fig. 758.—*Gyroceras ornatum.* Devonian.

In *Hercoceras* the shell is discoidal, with contiguous whorls and a wide umbilicus. The aperture is contracted; the sutures are simple; the siphuncle is submarginal and external; and the surface is adorned with transverse striæ or a row of projecting tubercles. The two known species are Silurian.

In the genus *Nautilus* itself (fig. 759) the shell is involute or discoidal, consisting of a few whorls coiled into a flat spiral, the volutions being in contact, and the last turn of the shell commonly more or less concealing the previous ones. In the young condition of the shell a central vacuity exists behind the conical initial chamber; but in the typical forms of the genus this becomes ultimately filled up by a secondary deposit of shell, or becomes concealed by the later volutions. The body-chamber is capacious, and the aperture is simple and has a ventral sinus. The

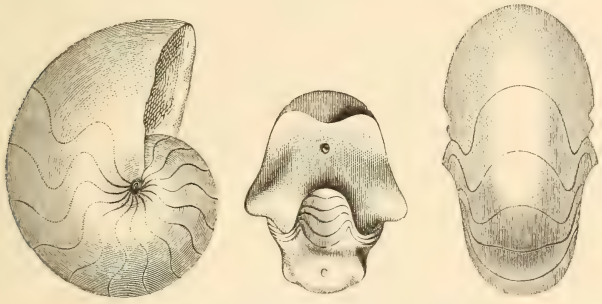


Fig. 759.—*Nautilus Danicus.* Upper Cretaceous.

septa are concave forwards, and the suture-lines are simple or may show a slight ventral or dorsal "lobe." The siphuncle is subcentral in position, or may be placed between the centre and either the ventral or the dorsal margin, and it is never contracted by internal deposits; while the septal "necks" are always short. The surface may be quite smooth (*Lævigati*), or adorned with transverse striæ (*Striati*), or with markedly distinct ribs (*Radiati*).

The genus *Nautilus* has been split up into a number of minor

groups, to some of which a generic value is now usually attached. Using the name in the wide sense in which it has been commonly employed, the genus may be said to range from the Ordovician to the present day; but the older types are almost certainly not congeneric with those of later periods.

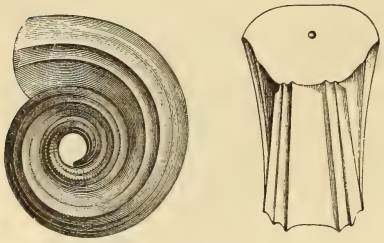


Fig. 760.—*Nautilus* (*Vestinautilus*) *Koninckii.* Carboniferous.

The name of *Discites* is given to forms generally included in the comprehensive genus *Nautilus*, in which the shell is widely umbilicated, with a persistent central vacuity; the volutions being four-sided, and the septa showing a deep ventral lobe. The forms of this type are Carboniferous. *Temnocheilus* (Devonian to Trias) and *Trematodiscus* (Carboniferous) likewise include widely umbilicated Nautili, in which the centre is perforated. A similar condition of parts exists in *Vestinautilus* (fig. 760), but in this type the whorls are trapezoidal in section and are very wide towards the aperture. The outer side of the shell is strongly keeled with lateral longitudinal ribs separated by a dorsal furrow. The genus is confined to the Carboniferous rocks.

Fig. 761. — *Bactrites elegans*, Devonian, Germany, of the natural size. (After Sandberger —copied from Zittel.)

Lastly, in *Aturia* the shell is involute and destitute of an umbilicus; and the sutures are strongly bent in a zigzag manner, with a deep lateral "lobe." The siphuncle is marginal and is placed on the internal side of the shell, the septal "necks" (fig. 743, *si*) being very long and being invaginated in such a manner as to form a complete siphuncular investment. The known species of *Aturia* are found in the Eocene and Miocene deposits.

Family 11. Bactritidæ. — This family includes only the genus *Bactrites* (fig. 761), in which the shell is straight and conical, with a circular or elliptical section, resembling that of *Orthoceras* in form. The siphuncle is delicate and marginal in position; and the septal necks are long and funnel-shaped. The sutures are undulated, with a backwardly-directed sinus corresponding with the siphuncle. Owing to the characters of the suture-lines, the genus *Bactrites* has been regarded as related to the

Goniatites, and as representing an ancient type of the Ammonoids, but it is now generally placed among the Nautiloids. The species of the genus are Silurian and Devonian.

Prosiphonate Nautiloids.

All the groups of the Nautiloids which have been previously considered are "retrosiphonate," having the septal necks directed backwards. On the other hand, the genera *Nothoceras* and *Bathmoceras* are "prosiphonate," the septal necks being directed towards the aperture of the shell. The genus *Bathmoceras* is Ordovician, and is characterised by the possession of a straight cylindro-conical shell, the septate portion of which is always truncated. The aperture is simple, and the siphuncle is marginal, and is ensheathed by numerous short invaginated funnels derived from the closely-set septa. In the Silurian genus *Nothoceras* the shell is nautiloid and widely umbilicated; the sutures are simple and concave; the siphuncle is ventral in position; and the septal necks are short and are directed forwards.

CHAPTER XLIII.

TETRABRANCHIATE CEPHALOPODS—continued.

Sub-Order II. Ammonoidea.

In this division of the Tetrabranchiate Cephalopods, the shell is usually rolled up into a spiral disc, but may be turreted, straight, hook-like, &c. The aperture may be simple, or may be furnished with lateral and ventral processes. The siphuncle is slender, cylindrical, marginal in position, and never contracted internally by shelly deposits. The septal "necks" are generally directed forwards, though in some forms (*e.g.*, *Goniatitidæ*) the reverse of this obtains. The septa are more or less folded or lobed, and the sutures are waved, angulated, or bent into "lobes" and "saddles." The structures known as the "Aptychus" and "Anaptychus" are commonly present. Lastly, the shell commences with a globular or inflated "protoconch," which is more or less clearly constricted off from the first septal chamber (fig. 744, D—G).

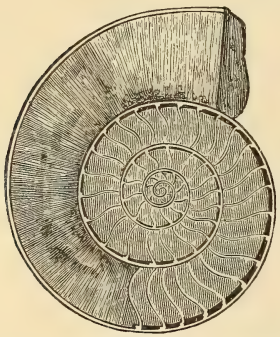


Fig. 762. — Section of *Arietites obtusus*, from the Lias, showing the long body-chamber.

The general structure of the shell and its mode of development have been already treated of (see p. 829 and p. 832); but there are some special features in the shell of the *Ammonoidea*, as compared with that of the *Nautiloidea*, which require consideration here.

The *body-chamber* of the *Ammonoidea* is of variable size, but in a number of forms it is remarkable for its great length as compared with its diameter (fig. 762), this implying that the body of the animal was very long and narrow. In some cases, indeed, the body-chamber may occupy an entire volution of the shell, or even a volution and a half.

The *aperture* of the shell in the Ammonoids is commonly furnished with lateral extensions or "ears," while its ventral or external side may be prolonged into a long pointed process or lobe. In this way a kind of cowl is sometimes formed above the aperture, and the width of the opening may be considerably contracted by the inward bending of these lobes (fig. 763). In the *Goniatitidæ* and *Clymeniidæ* the aperture resembles that of *Nautilus* in being simple, with a ventral sinus. In many cases the shell exhibits at intervals transverse ridges or contractions ("varices"), which represent the periodically formed mouths of the shell.

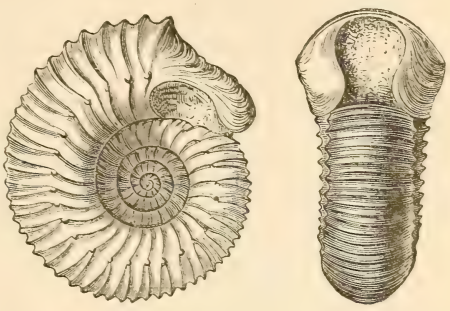


Fig. 763.—*Stephanoceras Brackenridgii*, viewed laterally and in front, showing the extensions of the margin of the aperture. Jurassic.

The *ventral* and *dorsal* sides of the shell of the Ammonoids cannot be always determined with certainty. There are, however, strong grounds for considering the external or convex side of the bent shells to be ventral, while the concave or internal side is dorsal.

The siphuncle in the Ammonoids is always cylindrical, and is never furnished internally with secondary calcareous structures resembling the "obstruction-rings" of many Nautiloids. Usually the sheath of the siphuncle is calcified, so that a continuous shelly tube is produced. The siphuncle commences by an inflated portion (fig. 764, *a*), which indents the protoconch (*pr*) on one side; and it is, to begin with, either internal or central in position. In the majority of the Ammonoids the siphuncle ultimately comes to be placed on the external margin of the shell (fig. 764, *si*), but in the *Clymeniidæ* it remains internal. The septal "necks" of the Ammonoids are variable in their development, as also in position.

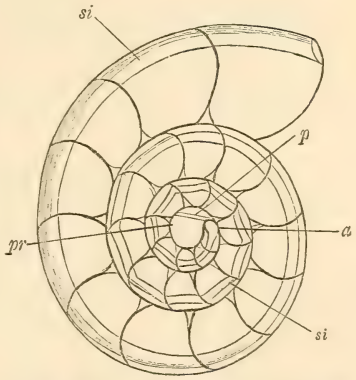


Fig. 764.—Section of *Ammonites* (*Cosmoceras*) *Parkinsoni*, in the mesial plane, showing the "prosiphon" (*p*), the siphuncle (*si*) with its dilated commencement (*a*), and the protoconch (*pr*). (After Munier-Chalmas.)

In most cases the shell is "prosiphonate," the septal necks being directed forwards, and being at the same time usually feebly developed. In the *Clymeniidæ* and *Goniatitidæ* the shell is "retrosiphonate," the septal necks being directed backwards; and in the former family these structures are so largely developed that they extend from one septum to the next behind.

The septa of the first-formed chambers of the shell of the Ammonoids are simply curved, or may be more or less bent, whereas in the adult portion of the shell they are always undulated or folded, the degree to which this takes place varying in different types. In the more specialised forms of the Ammonoids the septa "are nearly flat in the middle, and folded round the edge (like a shirt-frill) where they abut against the outer shell-wall" (Woodward). The result of this is that the "sutures," or edges of the septa, appear on the sur-

Fig. 765.—One-half of the suture of *Ammonites* (*Amaltheus*) *Truellei*; D, Siphonal or ventral lobe, traversed by the siphuncle (x); L, Superior-lateral lobe; E, Inferior-lateral lobe; A^1, A^2, A^3, A^4, Auxiliary lobes; S D, External saddle; S L, Lateral saddle; S^1, S^2, S^3, S^4, Auxiliary saddles.

face of the shell in the form of angulated, lobed, or foliaceous lines (fig. 765).

The angulated or digitated portions of the suture which are directed backwards, away from the mouth of the shell, are called the "*lobes*." The elevations between the "lobes," which point towards the aperture of the shell, are called the "*saddles*." These parts (fig. 765), as seen in one of the spirally-coiled Ammonoids, have the following arrangement: In the middle of the convex or ventral side of the shell is a single unpaired lobe, which is traversed mesially by the siphuncle, and is termed the "external," "ventral," or "siphonal" lobe (D). The lobe on each side of this (L) is known as the "superior-lateral lobe." The lobe on each side next to this again (E) is the so-called "inferior-lateral lobe"; and the lobes which follow this (of a variable number) are distinguished as the "auxiliary lobes" (A^1, A^2, A^3, A^4). Lastly, there is a second unpaired lobe immediately opposite to the ventral lobe, placed upon the concave side

of the shell, and known as the "internal," "dorsal," "antisiphonal," or "columellar" lobe. The "saddles" are similarly subdivided and distinguished. Between the ventral and superior-lateral lobes comes the "external saddle" (s d). Next to this, between the superior-lateral and inferior-lateral lobes, is placed the first "lateral saddle" (s l), followed on each side by a variable number of "auxiliary saddles" (s^1, s^2, s^3, s^4).

Associated with various forms of Ammonoids, sometimes situated within the body-chamber of the shell, or at other times wholly detached, are found the peculiar bodies to which the name of "Aptychi" has been applied. A typical *Aptychus* (figs. 766, 767)

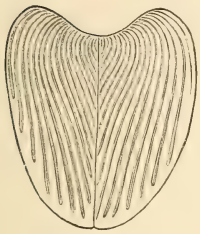


Fig. 766.—*Aptychus* (*Trigonellites*) *lamellosus*. Jurassic. (After Woodward.)

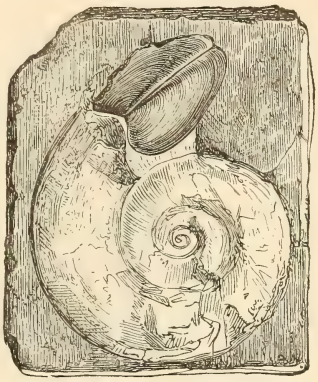


Fig. 767. — *Aptychus carinatus*, within the body-chamber of an Ammonite.

consists of two bilaterally symmetrical halves, which are somewhat semicircular in shape, and are apposed to one another by their straight inner margins, which are destitute of teeth. In some cases the *Aptychus* is thin and horny, but it is usually more or less extensively calcified, and its thickness is sometimes considerable. In the thick shelly types, the principal layer of the *Aptychus* has a peculiar cellular structure. The surface may be smooth or variously sculptured, and the inner face is commonly marked by concentric lines of growth. In the bodies to which the name of *Synaptychus* has been given, the general structure is similar to that of *Aptychus*, but the two halves of the structure are fused in the middle line. Bodies of this type have been found in the body-chamber of species of *Scaphites*. In *Anaptychus*, again, the structure is a thin, apparently horny, undivided plate, which is concentrically striated. Bodies of this nature have been found in association with certain forms of Ammonites and Goniatites. Some of the fossils which have been

described as the cephalic bucklers of Phyllocaridan Crustaceans (such as some of the forms referred to *Cardiocaris* and *Spathiocaris*) are in reality the "Aptychi" of Goniatites. Many theories have been held as to the nature of the "Aptychi" of the Ammonoids, but there are only two views which can be regarded as at all probable. On one of these views, the Aptychi are to be regarded as protective plates developed in the walls of the nidamental gland, in which case all examples of Ammonites possessing these structures are necessarily females. The more probable theory, however, is that put forward by Sir Richard Owen—viz., that the Aptychus is formed by the deposition of horny matter or lime within a structure corresponding to the "hood" of the existing Pearly Nautilus. On this view the Aptychus would act as an operculum, when the animal was withdrawn within the shell. In those Ammonoids which are devoid of Aptychi it must be supposed that the "hood" remained permanently uncalcified, as it does in the Pearly Nautilus.

As regards their *zoological affinities*, the Ammonoids have been generally regarded as belonging to the Tetrabranchiate division of the *Cephalopoda*, in which case the shell, like that of the Pearly Nautilus, must have been external. It has, however, been also held that the Ammonoids are really referable to the Dibranchiate division of the Cephalopods, in which case the shell, like that of the existing *Spirula*, must have been internal. The grounds for this view are chiefly derived from the mode of development of the shell of the Ammonoids, which resembles that observed in *Spirula* —the protoconch being in each case inflated and destitute of a cicatrix, while a "prosiphon" is present. The "Aptychi" of the Ammonoids have also been compared to the "nuchal cartilages" of the Cuttle-fishes. Upon the whole, however, the balance of evidence is in favour of the reference of the Ammonoids to the *Tetrabranchiata*—the groups of the *Clymeniidæ* and *Goniatitidæ* affording a transition between the two great sections of the *Ammonoidea* and *Nautiloidea*.

As regards the general *distribution in time* of the *Ammonoidea*, the most ancient types of the group belong to the genus *Goniatites*, in the wide sense of this name, and are found in the highest Silurian and the lowest Devonian deposits. The genus *Clymenia*, which, like *Goniatites*, is comparatively simple in morphological type, is also found in Devonian strata. The earliest forms of the "Ammonites" are found in the Permo-Carboniferous rocks of India, but in other regions the earliest representatives of this great section of the Ammonoids appear in the Trias. In the Mesozoic period the Ammonoids undergo a vast development, the principal and most widely distributed type being that of the "Ammonites." In the Cretaceous rocks, however, numerous new and varied

generic types are found, such as *Baculites*, *Hamites*, *Turrilites*, *Ptychoceras*, &c. With the close of the Cretaceous period, the entire group of the *Ammonoidea* underwent an apparently sudden and all but complete extinction, no undoubted examples of this division of Cephalopods being known in any unequivocal Tertiary strata, with the exception of certain "Ammonites" which have been found in the Eocene deposits of California.

In the following brief summary of the families of the *Ammonoidea* the arrangement adopted by Zittel has been adhered to :—

Family 1. Clymeniidæ.—In this family the suture-lines show simple lobes and saddles (fig. 768) ; the septal "necks" are directed backwards, the shell being "retrosiphonate"; and the siphuncle is placed on the internal side of the shell.

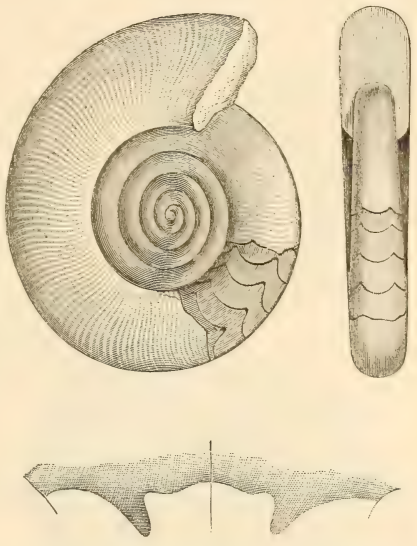


Fig. 768.—*Clymenia Sedgwickii*. Devonian. The lower figure shows the form of the suture.

The only genus included in this family is *Clymenia* itself (fig. 768), in which the shell is coiled into a flat spiral, the whorls of which are in contact. The inner side of each whorl is deeply excavated for the reception of the convexity of the preceding whorl, and the inner coils of the spire are exposed to view. The body-chamber is long ; the aperture has a ventral sinus ; and the surface is smooth or marked with fine transverse striæ. The sutures are simply folded or lobed, and the siphuncle is marginal, and is placed on the internal or concave side of the shell. The septal "necks" resemble those of the Pearly Nautilus in being directed backwards, and they are sometimes short, or at other times invaginated into one another. The protoconch resembles that of the *Goniatitidæ* in form, and is without a cicatrix. The known species of *Clymenia* are confined to the Upper Devonian rocks, some of the limestones of this age in Germany being spoken of as the "Clymenienkalk," owing to their being profusely charged with fossils of this genus.

Family 2. Goniatitidæ.—In this family the shell is spirally coiled, with more or less embracing whorls ; the suture-lines are

simply lobed or angulated, and are not foliaceous; the septal "necks" are directed backwards; and the siphuncle is marginal, and is placed on the external side of the shell. The "protoconch" (fig. 744, D and E) is inflated, and is devoid of a cicatrix.

This family comprises the comprehensive genus *Goniatites*, which has been divided by Hyatt into a considerable number of generic groups, which need not be characterised here. In all the forms included under the general name of *Goniatites* the shell (fig. 769) is discoidal, the extent to which the inner turns are exposed varying widely in different forms. In some cases there is a wide umbilicus, and the inner volutions are extensively exposed; whereas in other forms the umbilicus is much reduced in size, and the last whorl more or less completely conceals those which preceded it. The body-chamber is usually long; and the surface is generally smooth, but may be adorned with tubercles or ribs. The sutures show simple, sometimes rounded, sometimes angulated lobes and saddles. The septal "necks" resemble those of the *Nautilidæ* and of *Clymenia* in being directed backwards, the shell being thus "retrosiphonate." On the other hand, the slender siphuncle resembles that of the Ammonites in being

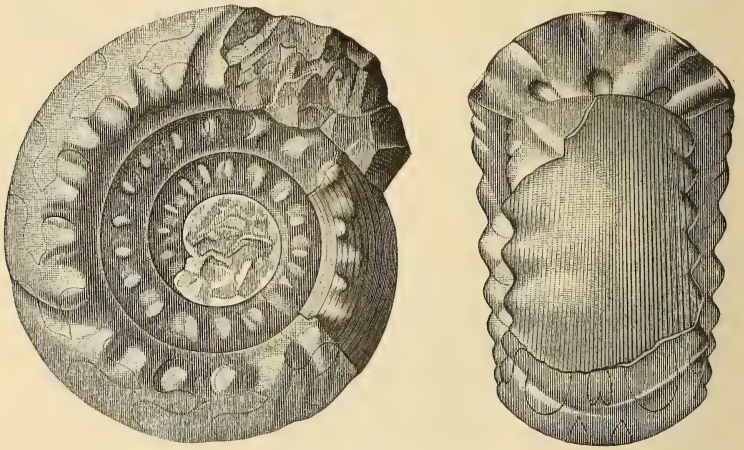


Fig. 769.—*Goniatites* (*Gastrioceras*) *Jossæ*. Carboniferous.

marginally placed on the *external* side of the shell. In some cases simple or divided "Aptychi" have been shown to be present.

The genus *Goniatites*, using the name in the wide sense, com-

prises about three hundred species, all of which are confined to the Palæozoic rocks. The earliest types appear in the later Silurian deposits, and have very simple suture-lines. In the Devonian and Carboniferous rocks numerous forms of Goniatites are known; and the latest representatives of the group are found in the Permo-Carboniferous beds of the Salt Range in India. In certain of the Devonian and Carboniferous Goniatites the sutures become complicated by the increase of the number of lobes and saddles, till a near approach is made to the structure of the septa in the Ammonites.

Family 3. Arcestidæ.—In this family the shell is discoidal, and the body-chamber is very long, extending over one or one and a half whorls. The surface of the shell is smooth, or may be adorned with transverse striæ, ribs, or folds. The suture-lines show very numerous lobes and saddles, and both of these are laterally incised, thus becoming foliaceous (fig. 770). No "Aptychus" is present. [In some forms a horny "Anaptychus" appears to have existed.]

The members of this, as of all the remaining families of the *Ammonoidea*, are distinguished from the *Clymeniidæ* and *Goniatitidæ* by the greater complexity of their septa and the more ornate form of the sutures resulting from this; while the septal "necks" are always turned forwards, and the shell is thus "prosiphonate." Formerly all these forms were grouped under a comparatively small number of genera, such as *Ceratites*, *Ammonites*, *Hamites*, *Turrilites*, *Baculites*, &c., distinguished principally by the mode of growth and the resulting form of the shell. By far the most important of these groups was the comprehensive genus *Ammonites*, embracing the great series of forms commonly known as "Ammonites." Through the researches of Hyatt, Neumayr, Mojsisovics, Waagen, von Zittel, and other well-known investigators, it has now been shown that the old genus *Ammonites* can no longer be maintained, but that the types formerly included under this name admit of a natural

Fig. 770.—Suture of *Cyclolobus Oldhami*, one of the *Arcestidæ*. Permo-Carboniferous, India. (After Waagen—copied from Zittel.)

division into a number of genera, which in turn constitute a number of distinct families. These modern divisions of the old genus *Ammonites* are distinguished by such morphological characters as the size of the body-chamber, the form of the sutures, the shape of the aperture, and the presence or absence of an "Aptychus." The mere *form* of the shell is a matter to which comparatively small weight is attached. Hence genera such as *Baculites*, *Turrilites*, and the like, in which the most obvious peculiarity is the external configuration of the shell, are now distributed, on the ground of their internal structure, among the different families into which the genus *Ammonites* has been broken up.

The three principal genera of the *Arcestidæ* are *Arcestes*, *Cyclolobus*, and *Lobites*. In the genus *Arcestes* the shell is involute, the last whorl being of large size, more or less completely concealing the inner whorls, from which it often differs in character. The umbilicus becomes constricted in course of growth, and is commonly completely closed by a callous deposit. The aperture is without lateral lobes, and the surface is smooth or furnished with fine transverse striæ. The species of *Arcestes* are almost exclusively Triassic, though early types (*Arcestes priscus*, Waagen) appear in the Permo-Carboniferous rocks of India, in which also is found the nearly allied genus *Cyclolobus* (fig. 770). The genus *Lobites* agrees with *Arcestes* in the general form of the shell, the long body-chamber, and the common closure of the umbilicus by a callosity. The surface, however, is commonly marked with radial folds (fig. 771), sometimes intersected by longitudinal striæ. The aperture may be simple, but is usually prolonged into a projecting hood. The species of this genus are confined to the Trias.

Fig. 771.—*Lobites delphinocephalus*. Trias.

Family 4. Tropitidæ.—In this family the shell is discoidal, with a long body-chamber, extending over more than one whorl. The surface is more or less richly ornamented, with radial ribs which often carry spines or tubercles. The sutures are foliaceous, the lobes and saddles being laterally incised. The principal genus of this family is *Tropites* itself, the species of which are found in the Trias principally, but survive into the Lias.

Family 5. Ceratitidæ.—In this family the form of the shell is variable, and its surface is ornamented with ribs or tubercles. The body-chamber is short, not extending over more than one-half or three-quarters of a volution. The sutures mostly show simple non-serrated "saddles," while the "lobes" are denticulated (fig. 772). The aperture is simple, and an "Aptychus" is not known to have been present.

The type of this family is the genus *Ceratites* (fig. 772), in which the shell is discoidal, the whorls in contact, and the inner volutions exposed to view. The lobes of the suture are denticulated or crenulated, while the saddles are simply rounded. The genus is characteristically Triassic, and the majority of the species are found in the Muschelkalk. In the Triassic genus *Trachyceras* (fig. 773) the general characters resemble those of *Ceratites*, but the saddles are in general laterally incised instead of being quite simple.

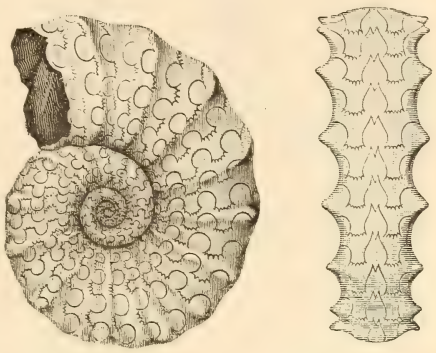


Fig. 772.—*Ceratites nodosus.* Muschelkalk (Middle Trias).

The preceding genera possess a discoidal shell, the whorls of which are in contact, but there are three Triassic genera included in this family in which the form of the shell is different. Thus, in *Choristoceras* the shell forms a flat spiral, the inner whorls of which are contiguous, while the last whorl is disjunct. In *Cochloceras*, again, the shell is turreted, while there is the additional peculiarity that the lobes, as well as the saddles, of the suture are simple. Lastly, in *Rhabdoceras* the shell is straight, the lobes of the suture being likewise free from denticulations.

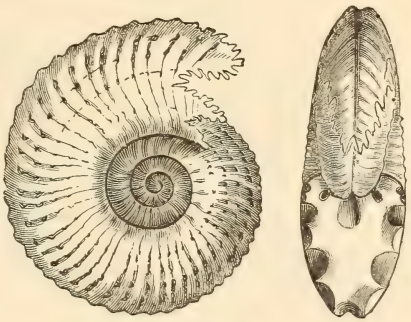


Fig. 773.—*Trachyceras Aon.* Trias.

Family 6. Cladiscitidæ.—In this family the shell is discoidal, and the body-chamber is long, extending over one whorl or thereabouts. The shell is thick and laterally flattened, the surface being spirally striated or smooth. The suture shows foliaceous saddles and finely incised lobes. This family was founded by Zittel to include certain Triassic "Ammonites," most of which belong to the genus *Cladiscites* itself.

Family 7. Pinacoceratidæ.—The shell in this family has the form of a compressed disc, usually with a smooth surface. The body-chamber is short, occupying from a half to two-thirds of the

last volution. The suture has very numerous lobes and saddles, which are sometimes incised, sometimes comparatively simple, one or more adventitious lobes being usually present. An "Aptychus" is not known to have existed.

Fig. 774.—Side-view of *Phylloceras heterophyllum*. Jurassic.

The genus *Pinacoceras* itself includes a number of Triassic "Ammonites," which sometimes attain to a great size (a yard or more in diameter), and are distinguished by the extraordinary complexity of the suture-lines. On the other hand, in the genus *Sageceras*, though the sutures show very numerous lobes and saddles, this complexity does not exist, the saddles being tongue-shaped and entire, while the lobes are simply indented. The species of this genus are chiefly Triassic, but early types appear in the Permo-Carboniferous ("Salt-Range Group") of India.

Family 8. Phylloceratidæ.—In this family the shell (fig. 774) is discoidal, the body-chamber occupying from one-half to three-fourths of a volution. The surface is smooth or adorned with

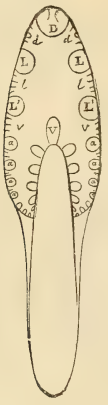


Fig. 775.—Outline of *Phylloceras heterophyllum*, showing the lobes and saddles. D, Siphonal lobe; L, Superior-lateral lobe; L′, Inferior-lateral lobe; *a a*, Auxiliary lobes; V, Antisiphonal lobe; *d*, External saddle; *l*, Lateral saddle.

Fig. 776.—Suture-line of *Phylloceras heterophyllum*. D, Siphonal lobe; L, Superior-lateral lobe; L′, Inferior-lateral lobe; *a a*, Auxiliary lobes; *d*, External saddle; *l*, Lateral saddle.

transverse striæ; and the aperture is simple. The lobes and saddles of the suture-line (fig. 776) diminish gradually in size in proceeding from the external towards the internal side of the shell;

and the saddles terminate in bladder-shaped rounded ends. An "Aptychus" is not known to have been present.

The type-genus of this family is *Phylloceras*, comprising involute "Ammonites," with a widely expanded body-chamber, a compressed form, and either no umbilicus or a small one (fig. 774). The surface usually exhibits fine transverse striæ, which are directed forwards; and the external margin is never keeled or tuberculated. The aperture is simple, with short ventral lobes. The most characteristic feature, however, is the presence of numerous saddles, which gradually diminish in size from without inwards, and which end in rounded or bladder-shaped extremities (fig. 776). The species of *Phylloceras* range from the Lias to the Cretaceous rocks, but the genus is preceded in the Trias by allied types (*Megaphyllites*).

Family 9. Lytoceratidæ.—Shell extremely variable in shape; the body-chamber in the coiled types occupying from two-thirds to three-quarters of the last volution. The surface is adorned with simple, wavy, or nodose ribs, which may be straight or bent. The

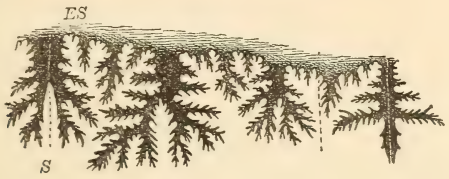


Fig. 777.—Suture-line of *Lytoceras Liebigi*, Jurassic. S, Siphonal lobe; ES, External saddle.

suture-line exhibits few (generally six), deeply incised lobes and saddles; the superior, and commonly also the inferior, lateral lobe being divided into two symmetrical halves, while the saddles may also be more or less clearly bilateral (fig. 777). An "Aptychus" is only known in the single genus *Baculites* (Zittel).

The type-genus of this family is *Lytoceras* itself, which, like all the "Ammonites," possesses a discoidal shell. As shown, however, by Neumayr, the characteristic suture-line of *Lytoceras* is possessed by a number of forms, such as *Turrilites*, *Baculites*, *Hamites*, &c., in which the shell may be coiled into a turreted spiral, or may be straight, hook-shaped, &c. The shell in *Lytoceras* (fig. 778) is discoidal and widely umbilicated, the whorls contiguous but hardly or slightly overlapping. The surface is usually adorned with radial lines of growth, or periodic contractions of the shell, with corresponding prominent fringed ribs ("fimbriæ") at intervals. The aperture is simple, with an internal lappet resting on the preceding whorl. The suture-line (fig. 777) is complex, the lateral lobes

and saddles being divided into small symmetrical digitations. The species of *Lytoceras* range from the base of the Lias to the middle of the Cretaceous system.

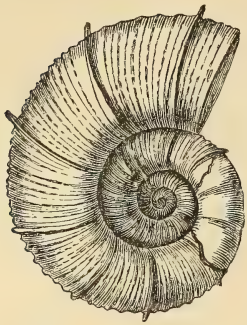


Fig. 778.—*Lytoceras fimbriatum.* Lias.

The genus *Macroscaphites* (fig. 779) comprises a portion of the forms included in the old genus *Scaphites*, and the suture-lines agree with those of *Lytoceras* and its allies in the fact that the lateral lobes are divided into two symmetrical halves. The first portion of the shell is coiled into a flat spiral, the volutions of which are in contact, but the last-formed portion of the shell is disjunct and is prolonged in a straight line, its terminal extremity being bent upwards and backwards. The species of this genus are confined to the Lower Cretaceous rocks.

In the genus *Hamites* (fig. 780) the shell is an extremely elongated cone, which is bent upon itself more than once in a hook-like manner, all the volutions being separate. The surface is usually adorned with transverse ribs, and the body-chamber is very long. The suture resembles that of the *Lytoceratidæ* in the fact that the superior-lateral lobe (as also commonly the inferior-lateral lobe) is divided into two symmetrical halves, the saddles also being bilaterally symmetrical. The species of *Hamites* range from the Neocomian to the Chalk, and some forms attain a considerable size. The Cretaceous (Neocomian) genus *Hamulina* differs from *Hamites* in the fact that the elongated shell is only bent once, its two portions being parallel to one another but not in contact. In the genus *Ptychoceras*, again, the shell (fig. 781) has the form of a greatly elongated cone, which is once bent upon itself, the two straight portions of the shell being in contact. The thicker limb of the shell is transversely ribbed; and the sutures have the same form as those of *Hamites*. The species of *Ptychoceras* are exclusively Cretaceous, and range from the Neocomian to the Gault.

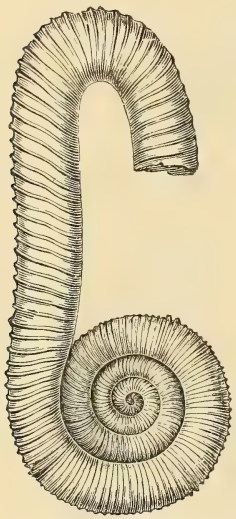


Fig. 779. — *Macroscaphites Ivanii.* Cretaceous. (Neocomian.)

In the genus *Turrilites* (fig. 782) the shell has the form of a

turreted spiral, being composed of volutions which pass obliquely round a central axis, an umbilicus being present or absent. The shell is usually sinistral, but is sometimes dextral. The surface is adorned with ribs or nodosities; and the lateral lobes of the suture-line are symmetrically divided. In *Turrilites* proper (fig.

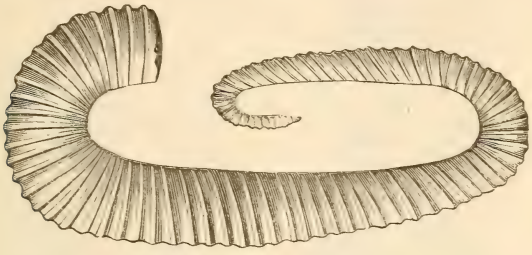


Fig. 780.—*Hamites rotundus*, restored. Cretaceous. (Gault.)

782) the volutions of the shell are in contact, whereas in *Helicoceras* the shell is coiled into an open spiral, the coils of which do not touch. Certain of the forms which have been placed in the genus *Heteroceras* (such as *H. polyplocum*) agree in the form of their sutures with *Turrilites*, from which they only differ in the fact that the terminal portion of the shell is coiled into an open spiral, the last whorl sometimes being prolonged in a straight line. All the types in question are Cretaceous, and range from the Neocomian to the Chalk.

Lastly, the genus *Baculites* is included in the family *Lytoceratidæ* from the form of its suture-lines, the superior-lateral lobes being symmetrically divided. The shell in this genus (fig. 783) is in the form of a straight elongated cone, with a long body-chamber, the aperture of which is simple and is prolonged ventrally. In some forms a divided "Aptychus" has been shown to exist. The species of this genus range from the Neocomian to the highest beds of the Chalk.

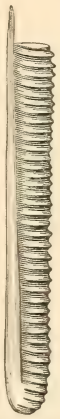


Fig. 781.—*Ptychoceras Emericianum*, reduced in size. Neocomian.

Family 10. Ptychitidæ. — This family includes forms of "Ammonites," of variable shape, the spirally coiled shell being flat or ventricose, with a wide or narrow umbilicus. The body-chamber occupies from two-thirds to three-fourths of a volution. The sutures are sometimes simply angulated and resemble those of the Goniatites; or the saddles are

round and the lobes denticulated, as in *Ceratites;* or both saddles and lobes are incised. No "Aptychus" is present (Zittel).

The genera included in this family are mostly Triassic, the type-

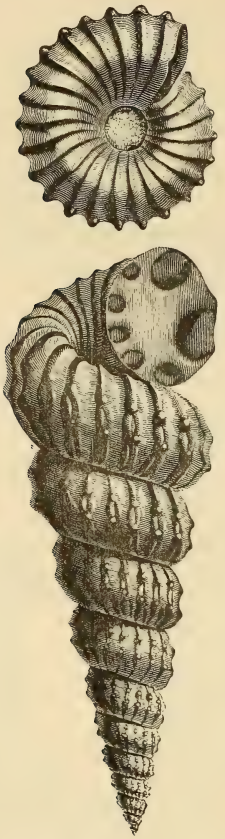


Fig. 782.—*Turrilites catenatus.* The lower figure represents the entire shell; the upper figure represents the base of the shell seen from below. Gault.

Fig. 783.—*Baculites anceps*, showing part of the body-chamber and a portion of the septal chambers. Chalk.

genus being *Ptychites* itself, in which the sutures have both the lobes and the saddles incised.

Family 11. Amaltheidæ.—This family includes "Ammonites," in which the shell is discoidal and laterally compressed (fig. 784, 785), and the last whorl conceals a considerable portion of the preceding volutions. The body-chamber occupies about two-thirds

of the last volution. The external side of the shell is acute, or is provided with a projecting keel, which is often hollow. The sutures are usually deeply incised, but may resemble those of *Ceratites* in form. A horny "Anaptychus" has been shown to exist in a number of forms.

The type-genus of this family is *Amaltheus* itself, in which the shell (figs. 784, 785) is furnished along its external margin with an

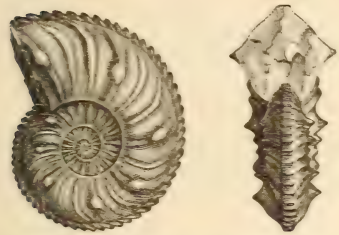


Fig. 784.—*Amaltheus* (*Ammonites*) *margaritatus*. Lias.

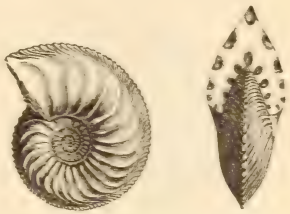


Fig. 785.—*Amaltheus* (*Ammonites*) *cordatus*. Jurassic (Coral Rag).

acute or transversely plaited keel. The surface may be smooth, striated, or transversely ribbed. The aperture is furnished with a ventral process, and the sutures have deeply incised lobes and saddles. Numerous species of this genus are found in the Jurassic rocks, beginning in the Lias.

Nearly allied to the preceding is the genus *Schloenbachia* (figs. 786, 787), in which the external side is broad, and is furnished with a strong median keel, in the hollow of which the thick siphuncle is usually contained. The surface is transversely ribbed, and the aperture is falciform, and is provided on its ventral side with a forwardly directed process. The species of this genus are exclusively Cretaceous, and range from the Neocomian to the Chalk.

Fig. 786.—Side-view of *Schloenbachia Roissyana*. Cretaceous.

Fig. 787.—End-view of *Schloenbachia crista*. Cretaceous.

In the Cretaceous genus *Buchiceras* the external edge of the shell is acute or keeled, but the sutures resemble those of *Ceratites* so closely that the forms of this type were formerly referred to the latter. Lastly,

the genus *Oxynoticeras* includes a number of Jurassic and Cretaceous "Ammonites," which differ from those comprised in *Amaltheus* chiefly in the form of the suture-lines.

Family 12. Ægoceratidæ.—The shell in this family of "Ammonites" is discoidal, compressed, and usually widely umbilicated; the surface generally with simple transverse ribs. The body-chamber occupies about three-fourths of the last volution, and the aperture is without lateral extensions. The suture is incised, with two lateral lobes, incompletely developed auxiliary lobes, and a bifurcated antisiphonal lobe. An "Anaptychus" is present (Zittel).

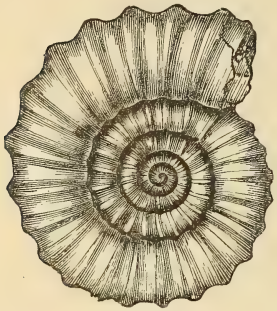


Fig. 788.—*Ægoceras capricornum.* Lias.

The type-genus of this family is *Ægoceras* (fig. 788), in which the surface shows simple transverse ribs spread out or split ventrally. The external side of the shell is rounded, without either a median keel or furrow. The species of this genus are confined to the Lias. The most important genus in this family is, however, *Arietites* (fig. 789), in which the shell is flat and discoidal, widely umbilicated, and many-whorled. The external margin is more or less flattened, and is provided with a median keel bordered by a lateral furrow on each side. The surface has simple straight ribs, which often have tubercles developed on them near the ventral margin. The body-chamber is long (fig. 762), and occupies one volution or more. A large number of species are known, all of which are confined to the Lower Lias, *A. Bucklandi*, *A. obtusus*, *A. bisulcatus*, and *A. rotiformis* being familiar species. If the name of *Ammonites* is to be employed at all as a generic designation, it must be for the forms here in question.

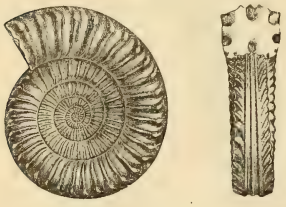


Fig. 789.—*Arietites* (*Ammonites*) *bisulcatus*, reduced in size. Lias.

Family 13. Harpoceratidæ.—In this family the shell (fig. 790) is discoidal, compressed, and umbilicated; the external margin is obtusely or acutely keeled; and the surface is adorned with falciform ribs or striæ. The aperture is falciform, and is furnished with rounded auricles and a long, pointed, ventral process. The suture is digitated, and the antisiphonal lobe is undivided. A calcified "Aptychus" is present.

The type of this family is the genus *Harpoceras*, of which very

numerous species are known, none of which transcends the limits of the Jurassic system. Familiar forms are the *H.* (*Hildoceras*) *bifrons*

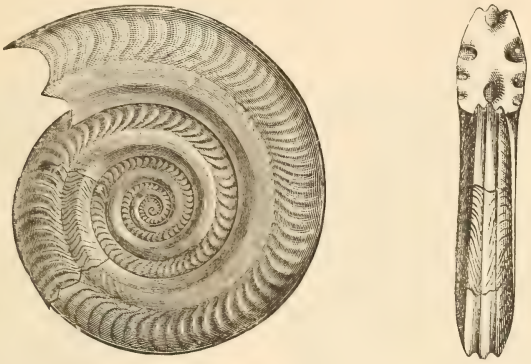


Fig. 790.—*Harpoceras* (*Hildoceras*) *bifrons*. Lias.

(fig. 790) and *H. serpentinum* of the Upper Lias. Allied to *Harpoceras* is the Jurassic genus *Oppelia*, in which the shell is involute, and the umbilicus is much reduced in size.

Family 14. Haploceratidæ.—In this family the shell is discoidal, with a wide or narrow umbilicus; the external margin being rounded, or in a few cases feebly keeled. The surface is adorned with fine lines of growth or curved ribs, commonly with falciform constrictions or varices. The aperture has feebly developed auricles; the suture-line is deeply incised; and an "Aptychus" has hitherto been recognised in a few forms only.

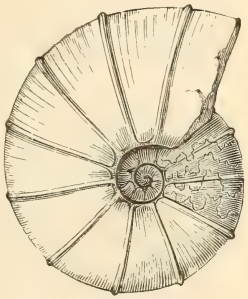


Fig. 791.—*Desmoceras* (*Ammonites*) *ligatum*. Cretaceous (Neocomian).

The family of the *Haploceratidæ* ranges from the Lower Jurassic rocks to the Chalk, and the principal genera are *Haploceras* and *Desmoceras* (fig. 791).

Family 15. Stephanoceratidæ.—The form of the shell in this family is variable, but the external margin is in general broad and rounded, and is never keeled; while the surface is almost always adorned with transverse ribs, which may carry tubercles, and usually bifurcate near the ventral border (fig. 792). The body-chamber occupies from one-half to two-thirds of the last volution. The aperture is commonly furnished with wide lateral extensions or lappets, which may be inflected to form a sort of cowl (fig. 763). The

lobes and saddles of the sutures are incised, and a calcified "Aptychus" is present.

In *Stephanoceras* itself (792) the shell is discoidal and usually widely umbilicated, and the surface is ornamented with strong ribs,

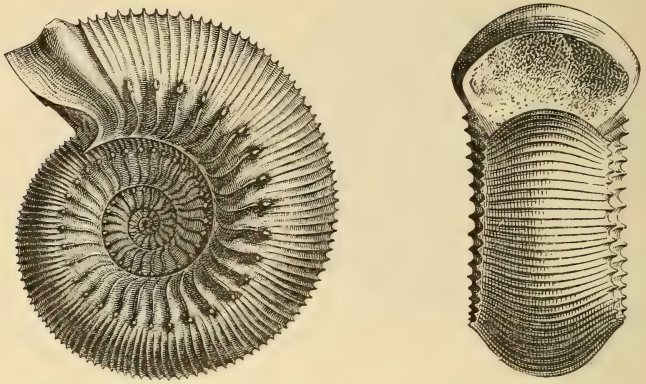


Fig. 792.—*Stephanoceras* (*Ammonites*) *Humphresianum*. Inferior Oolite.

which are simple internally, but become once or more divided on approaching the external border; the point of bifurcation being in general marked by the development of a more or less prominent

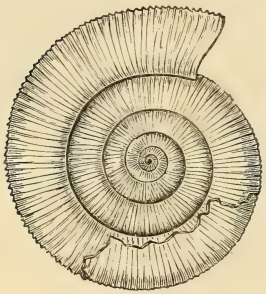


Fig. 793.—*Cœloceras* (*Ammonites*) *annulatum*. Lias.

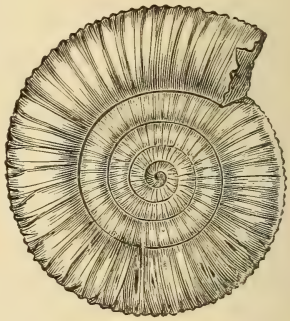


Fig. 794.—*Cœloceras* (*Ammonites*) *commune*. Lias.

tubercle. The species of the genus are confined to the Jurassic rocks.

Very closely allied to the preceding is the genus *Cœloceras*, but the types included under this name have a long body-chamber (extending over more than one whorl), while the aperture of the shell

is simple and without side-lappets. The surface-sculpture is similar to that of *Stephanoceras*. All the species of *Cœloceras* are found in the Lias, two well-known forms being *C.* (*Ammonites*) *annulatum* (fig. 793), and *C.* (*Ammonites*) *commune* (fig. 794).

In *Cosmoceras* (fig. 795) the shell is discoidal and the surface-ribs are bent forwards, and often have tubercles or spines developed along their external ends. The aperture of the shell is furnished with long lateral extensions, which may disappear with age. The species of *Cosmoceras* are Jurassic and Lower Cretaceous.

Fig. 795.—*Cosmoceras* (*Ammonites*) *Jason*, reduced in size. Jurassic (Oxford Clay).

In *Perisphinctes* (fig. 796) the shell is discoidal, and usually widely umbilicated, with a rounded external border. The surface-ribs divide, each, near the siphonal margin, into two or more branches. The body-chamber extends over two-thirds or the whole of the last whorl, and the aperture is simple, with lateral extensions or auricles.

Fig. 796.—*Perisphinctes* (*Ammonites*) *Martinsi*. Inferior Oolite.

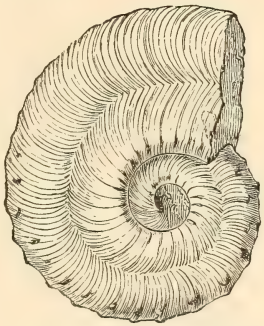


Fig. 797.—*Hoplites* (*Ammonites*) *falcatus*. Cretaceous.

A very large number of species of this genus are known, ranging from the Inferior Oolite to the Lower Cretaceous.

In the genus *Hoplites* (fig. 797) the shell differs from that of *Perisphinctes* in being involute, with the umbilicus narrow, and the whorls high. The surface-ribs spring from tubercles near the umbilical margin, which divide as they proceed outwards, and are generally interrupted by a broad furrow along the line of the external border of the shell. The species of this genus are characteristic of the Cretaceous system.

In *Acanthoceras* the shell (fig. 798) is discoidal and umbilicated, and the sculpture consists of strong, straight, undivided, or divided

ribs, which increase in width in proceeding from the umbilicus towards the external margin, and are often adorned with tubercles. In the genus *Aspidoceras*, again, the shell (fig. 799) may be flat and widely umbilicated; or it may be inflated and involute, with a narrow umbilicus. The sculpture consists of one or two rows of tubercles, which occasionally become obsolete in late life, while ribs are as a rule only present in young examples. The numerous species of

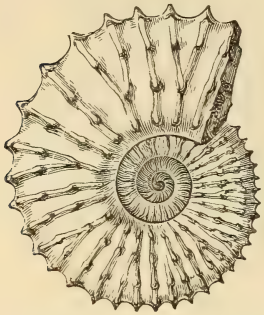


Fig. 798.—*Acanthoceras Deverianum*. Cretaceous (Lower Chalk).

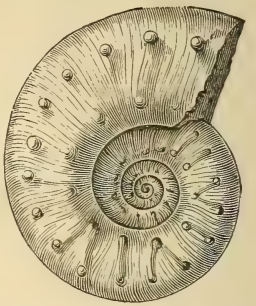


Fig. 799.—*Aspidoceras longispinum*. Jurassic (Kimeridge Clay).

Acanthoceras are wholly Cretaceous, while *Aspidoceras* ranges from the Middle Jurassic to the Lower Cretaceous. Allied genera are *Simoceras* and *Peltoceras*, both of which are confined to the Jurassic series.

All the preceding forms of the *Stephanoceratidæ* possess a spirally-coiled shell, the volutions of which are contiguous and lie in a single plane; and all belong to the great group of the "Ammonites." There are, however, other types, with a variously coiled shell, which, as judged by their general morphological characters, appear to be properly referable here. Amongst the types in question is the genus *Scaphites*, as restricted by the removal to the *Lytoceratidæ* of the forms which constitute the genus *Macroscaphites*. In *Scaphites* proper the shell (fig. 800) consists of a series of volutions coiled into a flat spiral, but having the last whorl detached from the others, produced, and ultimately bent back in the form of a crosier. The suture-line shows several auxiliary lobes; and an "Aptychus" is present. All the known species of *Scaphites* are confined to the Cretaceous system.

Fig. 800.—*Scaphites æqualis*. Upper Cretaceous.

In the genus *Crioceras* (fig. 801) the shell is rolled into a spiral,

the turns of which lie in one plane, but the volutions are not in contact with one another. The surface-sculpture consists of transverse ribs, usually with rows of tubercles or short spines. The suture is much ramified, but only consists of four principal lobes, viz., a siphonal lobe, superior-lateral lobe, inferior-lateral lobe, and

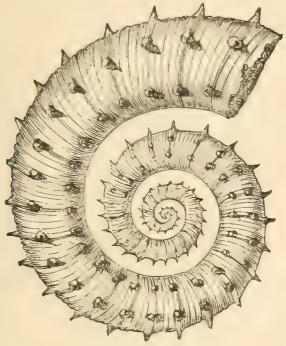


Fig. 801.—*Crioceras Emerici.* Cretaceous.

Fig. 802.—*Heteroceras Emerici.* Cretaceous.

antisiphonal lobe. The body-chamber is long, and the aperture is simple and without side-lappets. The species of *Crioceras* are Cretaceous, ranging from the Lower Greensand to the Gault. Some of the forms which have been placed under the genus *Heteroceras* appear to be nearly related to *Crioceras*. In these forms the first portion of the shell resembles *Turrilites* in being obliquely coiled and turreted, with contiguous whorls; but the last volution is detached from the rest, and is produced and recurved (fig. 802).

The forms for which the name of *Toxoceras* is employed have an elongated, arcuate or bow-shaped shell, which is not coiled into a

Fig. 803.—*Ancyloceras Matheronianum.* Gault.

spiral; and the structural characters agree with those of *Crioceras*. The species of *Toxoceras* are found in the Lower Cretaceous rocks; but it is not clear that the genus has not been founded upon broken examples of *Crioceras*.

Also very closely allied to *Crioceras*, if not absolutely identical with it, is the genus *Ancyloceras* (fig. 803), in which the shell agrees with that of the former in consisting in its earlier portion of several volutions, which are coiled into a flat spiral, but are not in contact with one another. The shell differs, however, from that of *Crioceras* in the fact that the last volution is produced at a tangent, and is ultimately bent back in the form of a crosier. The sutures are divided into six lobes, which are very unequal in size, and are digitated in a complex manner. The genus is Jurassic and Cretaceous, ranging from the Inferior Oolite to the Neocomian.

CHAPTER XLIV.

DIBRANCHIATE CEPHALOPODS.

The Dibranchiate Cephalopods or "Cuttle-fishes" are characterised as being *swimming animals, almost invariably naked, with never more than eight or ten arms, which are always provided with suckers. There are two branchiæ, which are furnished with branchial hearts; an ink-sac is always present; the funnel is a complete tube; and the shell (when present) is internal, or, if external, is not chambered.*

The Cuttle-fishes (fig. 804) are rapacious and active animals, swimming freely by means of the jet of water expelled from the funnel. The arms constitute powerful offensive weapons, being excessively tenacious in their hold, and being sometimes provided with a sharp claw in the centre of each sucker. They are mostly nocturnal or crepuscular animals, and they sometimes attain to a great size.

The general anatomy of the Cuttle-fishes has already been briefly discussed (see p. 821), and it only remains to allude shortly to certain points which possess a special palæontological interest. Under certain exceptionally favourable circumstances the outline of the body has been preserved in the fossil Dibranchiates, and in such cases the horny hooks with which the suckers are occasionally furnished may be recognisable, and it may even be possible to determine the number of the "arms." The mandibles of the Cuttle-fishes differ from those of the Tetrabranchiates in not being calcified, and these structures are therefore not preserved in the fossil condition. On the other hand, the Dibranchiates possess in the ink-sac a structure which is quite capable of petrifaction, the carbonaceous particles suspended in the "ink" being very indestructible. Hence the fossilised ink-bag of the Dibranchiates is of tolerably frequent occurrence.

The skeleton in the Dibranchiates may be rudimentary or wholly absent, as in the majority of the Octopods. In the female Argonaut, again, there is a delicate, involute, *external* shell, which is

secreted by the two dorsal arms, and has no connection with the mantle of the animal. In the great majority of the Dibranchiates, however, there exists an *internal* shell which is contained within the mantle, and varies in structure in different types. In some cases, the shell has the form of an elongated, horny, feather-shaped

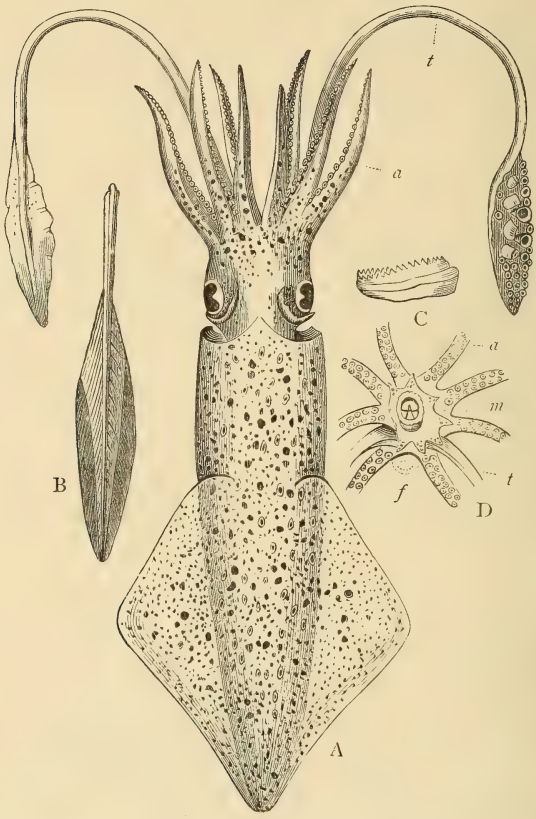


Fig. 804.—A, The Common Calamary (*Loligo vulgaris*), reduced in size: *a*, One of the ordinary arms; *t*, One of the longer arms or "tentacles." B, Skeleton or "pen" of the same, one-fourth natural size (after Woodward). C, Side-view of one of the suckers, showing the horny hooks surrounding the margin. D, View of the head from in front, showing the bases of the arms (*a*) and tentacles (*t*), the mouth (*m*), and the funnel (*f*).

body or "pen" (fig. 737, *b*), which is situated dorsally in a closed sac of the mantle. In other cases, as in *Sepia* (fig. 737, *a*) the internal shell is calcareous in composition. The posterior end of this skeleton may exhibit in a rudimentary form a chambered sac or "phragmacone," but in many cases no trace of this structure can

be detected. In the extinct family of the *Belemnitidæ*, the skeleton consists of a well-developed chambered cone (the "phragmacone"), which is divided by arched septa into a succession of air-chambers, the septa being pierced by a tube or "siphuncle." The phragmacone in this family is prolonged forwards on its dorsal side into a flattened "pen" (the "pro-ostracum"), while it is protected posteriorly by a solid calcareous investment or sheath (the "guard"). In the existing genus *Spirula* the shell is internal, but is reduced to the chambered "phragmacone," which is coiled into a flat spiral, the coils of which are not in contact (fig. 737, *c* and *d*).

The phragmacone commences in a globular or inflated "protoconch" or "initial chamber" (fig. 805, *pr*), which is distinctly constricted off from the first air-chamber, and which is devoid of a cicatrix. The siphuncle commences as a cæcal tube (*c*) pushed into the protoconch; and a "prosiphon" (*p*) is present. It will be thus seen that the protoconch of the Dibranchiates is essentially similar to that of the Ammonoids, a fact which has led some naturalists to the belief that the latter are truly Dibranchiate, and that their shell was therefore internal. In all the Dibranchiates in which a phragmacone is completely developed, the siphuncle is constantly *ventral* in position, and in *Spirula* it is consequently placed along the concave side of the shell.

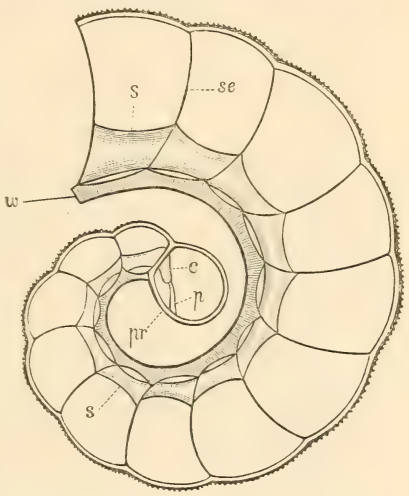


Fig. 805. — Longitudinal section of the shell of *Spirula Peroni*. *pr*, Protoconch; *p*, Prosiphon; *c*, Cæcal commencement of the siphuncle; *s s*, Siphuncle; *se*, One of the septa; *w*, Ventral wall of the shell. (After Munier-Chalmas.)

As regards their *classification*, the *Dibranchiata* are divided into two sub-orders, the *Octopoda* and the *Decapoda*, the former characterised by the possession of eight arms only, while in the latter there are eight comparatively short arms and two long arms or "tentacles." The *Decapoda* constitute the most important of these groups, and are divided by Fischer into the three sections of the *Phragmophora*, *Sepiophora*, and *Chondrophora*, in accordance with the nature of the skeleton.

As regards the distribution of the Dibranchiate Cephalopods in time, no Palæozoic types of the order have hitherto been detected.

The oldest known representatives of the order appear in the Trias, and belong to the extinct families of the *Belemnitidæ* and *Belemnoteuthidæ*. The *Belemnitidæ* show a great development in the Jurassic rocks, and in the same deposits occur the remains of Cuttle-fishes essentially similar to those now in existence (forms of the *Chondrophora*). The typical members of the *Belemnitidæ* disappear with the close of the Cretaceous period, but a few forms of this important Mesozoic family survive into the Tertiary. At the present day, the sole survivor of the section of the *Phragmophora* is the genus *Spirula*. The oldest types of the *Sepiophora* appear in the Tertiary deposits. In the following are given the characters and distribution in time of those families of the Dibranchiates which are known to occur in the fossil condition.

Sub-Order I. Decapoda.

The forms included in this sub-order invariably possess an internal shell, and the head is always furnished with eight equal "arms" and two longer "tentacles" (fig. 804, A). The mantle is usually furnished with lateral or terminal fins, and the suckers of the arms are pedunculate, or may be modified into horny hooks.

The sub-order is subdivided by Fischer into the three following families :—

1. *Phragmophora.*—Cuttle-fishes in which the skeleton is furnished with a "phragmacone," or chambered portion, in which a siphuncle is developed. *Ex. Spirula, Belemnites.*
2. *Sepiophora.*—Cuttle-fishes in which the skeleton is calcareous, but there is either no phragmacone, or a quite rudimentary one without a siphuncle. *Ex. Sepia.*
3. *Chondrophora.*—Cuttle-fishes in which the shell has the form of a horny "pen." *Ex. Loligo.*

Section A. Phragmophora.

In this section the shell consists of a "phragmacone," with or without certain accessory structures. The phragmacone (fig. 805) resembles the shell of the Tetrabranchiates in consisting of a succession of air-chambers separated by shelly partitions or "septa," which are perforated by a "siphuncle"; and it more particularly resembles the shell of the Ammonoids in the fact that the "protoconch" is inflated and is provided with a "prosiphon." The skeleton is, however, *internal*, and possesses also other peculiarities which are not found in the shell of any of the Tetrabranchiates. The only existing representative of this section is the genus *Spirula*, but numerous fossil forms are known. The *Phragmophora* may be divided into the following three families :—

Family 1. Spirulidæ.—This family includes only the recent genus *Spirula* (fig. 737, *c* and *d*, and fig. 805), in which the shell is reduced to the phragmacone. This is coiled into a flat spiral, the coils of which are not in contact, and it commences in an inflated protoconch. The septa between the successive air-chambers are concave; and the siphuncle is marginal, and is placed on the ventral or concave side of the shell. The siphuncle is completely enclosed within a series of septal "necks," which are directed backwards, and are long enough to reach from one septum to another. No fossil representatives of the genus have hitherto been recognised.

Family 2. Belemnitidæ.—In this family the shell has the form of a conical "phragmacone," with a ventral siphuncle (fig. 806, *a*), which is lodged within a solid fibrous calcareous sheath or "guard" (*b*), and which has its dorsal margin prolonged into a thin horny or shelly plate or "pro-ostracum" (*c*), corresponding with the "pen"

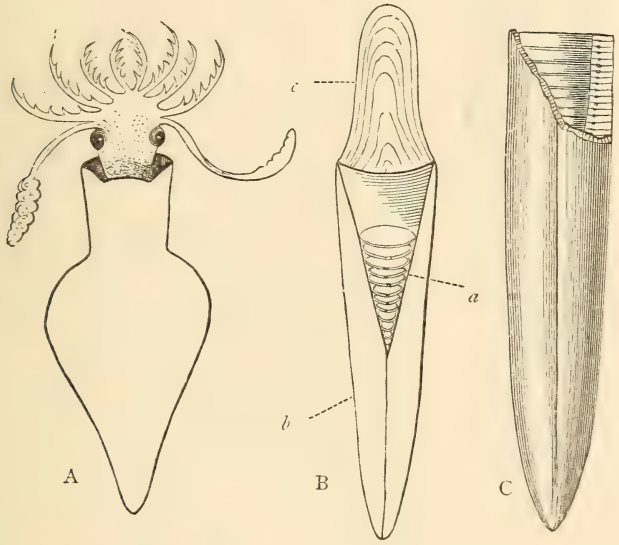


Fig. 806.—A, Restoration of the animal of the Belemnite; B, Diagram showing the complete skeleton of a Belemnite, consisting of the chambered phragmacone (*a*), the guard (*b*), and the horny pen (*c*); C, Specimen of *Belemnites canaliculatus*, from the Inferior Oolite. (After Phillips.)

of the *Chondrophora*. The arms in the *Belemnitidæ* were furnished with hooklets, and an ink-bag was present. The members of this family are all extinct, and range from the Trias to the Miocene Tertiary.

The most important genus in this family is *Belemnites* itself, in which the portion of the shell most commonly preserved is the

subcylindrical, conical, or fusiform "guard" or "rostrum." At its anterior broad extremity the "guard" is hollowed out into a conical excavation, termed the "alveolus" (fig. 807, *a*). Within the alveolus, in well-preserved specimens, is found the "phragmacone." This (fig. 807, *p*) consists of a conical series of chambers, enclosed in a thin proper wall (the "conotheca" of Huxley), and separated from one another by curved shelly partitions or "septa," which are perforated by apertures for the passage of the "siphuncle." The siphuncle is marginal, and traverses the middle of the ventral wall of the phragmacone. The outer or anterior chamber of the phragmacone is of tolerably large size; and the conotheca is prolonged forwards on its dorsal side into a horny or more or less calcified plate, known as the "pro-ostracum." This corresponds with the "pen" of the ordinary Cuttle-fishes, and from its extreme tenuity is never perfectly preserved, and, indeed, is completely wanting in the great majority of specimens.

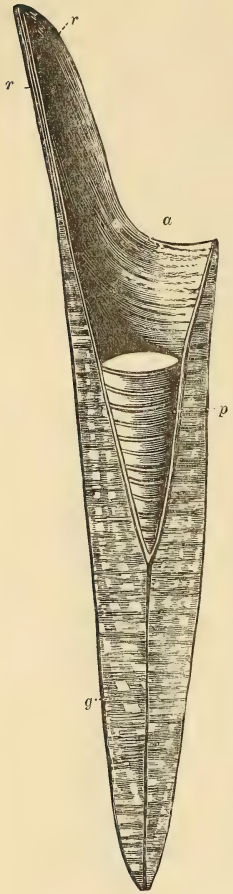


Fig. 807.—Diagram of Belemnite (after Professor Phillips). *r*, Horny or shelly pen or "pro-ostracum"; *p*, Chambered "phragmacone" in its cavity or "alveolus" (*a*); *g*, "Guard."

The "guard" of the Belemnites consists of prismatic calcareous fibres, which are directed perpendicularly to the surface, and radiate in all directions from an axial line, which is not strictly central, but is somewhat nearer the ventral than the dorsal side. The growth of the guard is effected by the deposition of successive conical layers or sheaths, which are secreted over the entire surface, but are thickest behind, and become gradually attenuated in front. The surface of the guard is smooth; or may be wholly or partially granulated or wrinked; or, again, may be marked with branched vascular impressions, which are especially conspicuous on the ventral side. In many cases a well-marked groove — the "ventral furrow"— runs from the edge of the alveolus backwards on the ventral side, extending for a short distance only, or reaching to the point of the guard (fig. 806, c). In many cases the apical portion of the guard shows two symmetrical grooves—the "dorso-lateral grooves"—which

diverge slightly and become shallower as they extend forwards, and which mark the dorsal side of the shell.

Between three and four hundred species of the genus *Belemnites* are known, the maximum development of the group taking place in the Jurassic rocks. The oldest forms appear in the Lower Lias, and the last in the Chalk, but the genus appears to have wholly died out with the close of the Cretaceous period.

According to Zittel, the following sections of the genus *Belemnites* may be recognised :—

1. *Acuarii.*—Guard conical, with two or three apical grooves, but without a "ventral furrow" or "dorso-lateral grooves." (*Ex. B. acuarius*, Upper Lias.)

2. *Canaliculati.*—Guard elongated, conical, or fusiform, with a deep "ventral furrow." (*Ex. B. canaliculatus*, Inferior Oolite, fig. 806, c.)

3. *Clavati.*—Guard elongated, more or less clavate posteriorly, without a "ventral furrow," but with well-marked lateral grooves. (*Ex. B. clavatus*, Lias.)

4. *Bipartiti.*—Guard slender, cylindrical, with or without a "ventral furrow," but with deep "dorso-lateral grooves." (*Ex. B. bipartitus*, Neocomian.)

5. *Hastati.*—Guard elongated, narrower in front, thicker behind, and terminating in a point posteriorly. A deep "ventral furrow" is present, together with shallow lateral grooves. (*Ex. B. hastatus*, Oxford Clay.)

6. *Conophori.*—Guard conical, pointed behind. No ventral furrow is present, but a corresponding furrow proceeds from the edge of the alveolus backwards on the dorsal aspect of the shell. Lateral grooves are wanting or feebly developed. (*Ex. B. conophorus*, Neocomian.)

7. *Dilatati.*—Guard short, laterally compressed, flattened or four-sided. A dorsal furrow, as in the preceding group, is present, and the lateral grooves are more or less developed. (*Ex. B. dilatatus*, Neocomian.)

Fig 808.—*Belemnitella mucronata.* Chalk.

Closely allied to *Belemnites* proper, and probably not generically separable, are the forms included under the name of *Belemnitella*. In these types (fig. 808) the guard is cylindrical, with a short pointed mucro behind. Two diverging dorso-lateral lines exist on each side; and there is a slit-like ventral furrow, which begins at the margin of the alveolus, but does not reach the hinder end of the same. The ventral side of the guard shows very well-marked vascular impressions. The known species of *Belemnitella* are confined to the Upper Cretaceous rocks.

The most ancient type of the *Belemnitidæ* is the genus *Aulacoceras*, which is found in the Upper Trias of the Alps. In this genus the guard is elongated and clavate in form, with a deep lateral groove on each side. The phragmacone is at least twice as long as the guard, and slowly increases in width anteriorly.

The siphuncle is marginal, enclosed in a calcareous sheath, and contracted where it pierces the successive septa. *Atractites*, also from the Alpine Trias, differs from *Aulacoceras* chiefly in the want of lateral furrows.

In the singular genus *Xiphoteuthis*, of the Lower Lias, the guard is cylindrical; the phragmacone is greatly elongated, and increases very slowly in width; and there is a narrow "pro-ostracum," which is at least five times as long as the guard.

In the Tertiary rocks, the family of the *Belemnitidæ* is represented by the genera *Belemnosis*, *Beloptera*, and *Spirulirostra*. The only known species of *Belemnosis* is found in the Eocene rocks (London Clay), and has a short obtuse guard, with a terminal pore. The phragmacone has horizontal septa and a marginal siphuncle. The genus *Beloptera* is also known by a single species only, and likewise occurs in the Eocene rocks. In this curious type the shell consists of two conical segments joined point to point, and further united by wing-like lateral expansions. The posterior portion of the skeleton represents the guard, while the phragmacone is lodged in the anterior portion.

Lastly, in the genus *Spirulirostra* (fig. 809) the skeleton consists of a triangular, pointed guard, which is hollowed out in front for the

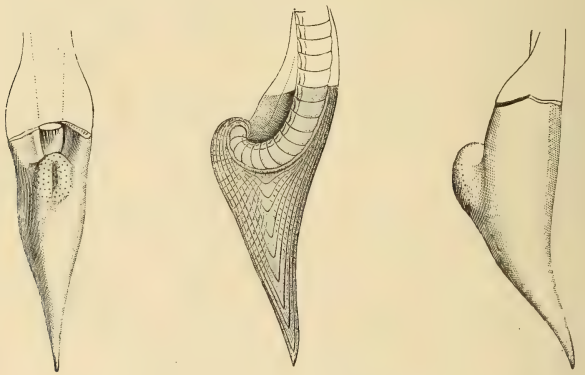


Fig. 809.—*Spirulirostra Bellardii.* Miocene Tertiary.

reception of a chambered portion or phragmacone. This latter is spirally bent, and the septa are pierced along its concave or ventral side by a marginal siphuncle. The only known species of *Spirulirostra* is found in the Miocene deposits of Italy.

Family 3. Belemnoteuthidæ.—In this family the skeleton is internal, and resembles that of the *Belemnitidæ* in consisting of a "guard," a chambered "phragmacone," and a thin shelly "pro-ostracum." The guard is, however, reduced to a thin calcareous

layer, which invests the conical phragmacone. The members of this family are confined to the Upper Trias and the Jurassic rocks, and the principal genus is *Belemnoteuthis* (fig. 810) itself. In the Oxford Clay, specimens of *Belemnoteuthis* have been found in which the outline of the soft parts has been more or less perfectly preserved. From these it is known that the animal had eight arms, with two "tentacles," furnished with horny hooks. The hinder end of the body was furnished with terminal fins; and there was a large ink-sac situated a little in front of the phragmacone. The phragmacone itself seems to have reached to nearly one-third of the length of the body.

Section B. Sepiophora.

In this section of the Decapods the skeleton is internal and is calcareous, consisting of a well-developed "pro-ostracum," terminating posteriorly in a rudimentary phragmacone and rostrum. No siphuncle is developed.

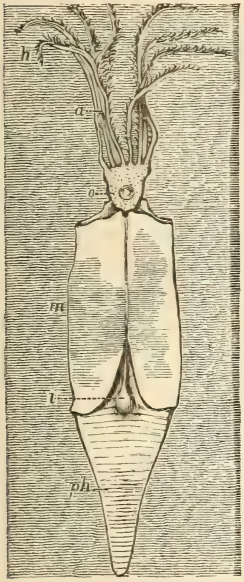


Fig. 810.—Restoration of *Belemnoteuthis*, from the Oxford Clay.

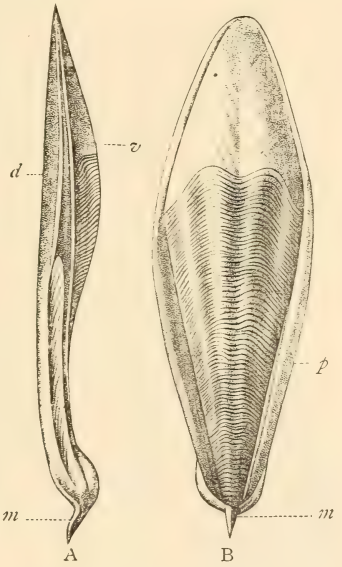


Fig. 811.—Side-view (A) and ventral view (B) of the shell of *Sepia Orbignyana*. *p*, "Pro-ostracum"; *m*, Mucro, hollowed out in front for the rudimentary phragmacone; *d*, Dorsal side of the shell; *v*, Ventral side. (After D'Orbigny.)

The type of this section is the existing genus *Sepia*, in which the shell ("sepion" or "sepiostaire") consists of an elongated, oval, calcareous "pro-ostracum" (fig. 811, *p*), which is rounded in front,

and terminates posteriorly in small pointed "mucro" (*m*). The front portion of the mucro is hollowed out, and contains a rudimentary "phragmacone," in which, however, a "siphuncle" is wholly wanting. The pro-ostracum forms the largest portion of the shell, and is thickened in front and concave on its inner side behind. The convex dorsal side is formed of two strata of comparatively dense calcareous tissue, partially separated by a chitinous lamella. The concave inner side, on the other hand, is formed of a large number of delicate parallel calcareous plates, which are not in contact, but are united by vertical pillars, giving rise to a spongy tissue, the spaces of which are filled by gases secreted by the animal. The rudimentary phragmacone is imperfectly chambered, and the minute "mucro" is the representative of the "guard" of the Belemnites.

A few fossil types of *Sepia* are known, the oldest appearing in the Eocene deposits. In the Eocene genus *Belosepia* the "sepion" is like that of *Sepia*, and has a short, slightly bent rostrum. Internally the rostrum is hollowed out for the reception of a chambered phragmacone, and on the inner side of this is an oblique funnel-shaped cavity, which is regarded by Munier-Chalmas as representing the siphuncle. Anteriorly the rostrum is continued into a calcareous pro-ostracum, the dorsal surface of which is rugose.

Section C. Chondrophora.

In this section of the Decapods the skeleton is internal, and has the form of a long, thin, pointed or feather-shaped "pen," which is not calcified, or only partially so, but is composed of a horn-like substance ("conchiolin").

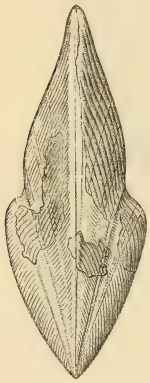


Fig. 812.—*Beloteuthis subcostata*. Jurassic (Lias).

This section includes a large number of the commoner Cuttle-fishes of the present day, such as the familiar Calamaries (*Loligo*, fig. 804). Various fossil forms are also known from the Jurassic and Cretaceous rocks, the "pens" of these being often accompanied by the remains of the ink-sac. The fossil "pens" consist generally partly of horny and partly of calcified lamellæ, and some of them attain a considerable size. A number of genera have been founded upon these fossil pens, such as *Phylloteuthis*, *Beloteuthis* (fig. 812), *Geoteuthis*, *Leptoteuthis*, *Plesioteuthis*, &c.; but the differential characters of these are not of sufficient importance to require discussion here. In some of these types, as in *Plesioteuthis*, the pen is very long and sword-shaped, and is without lateral wings. More commonly, as in *Beloteuthis* (fig. 812), the pen is

more or less feather-shaped, and consists of a central shaft bordered by lateral wings. In some cases, as in *Leptoteuthis* and *Plesioteuthis*, the actual impression of the body of the animal is preserved, and from such examples it is known that the arms were not furnished with horny hooks.

Sub-Order II. Octopoda.

The forms included in this section of the Dibranchiates are characterised by the possession of eight equal arms, the internal skeleton being rudimentary or absent. The suckers of the arms may be modified into horny hooklets. In the female of the Paper Nautilus (*Argonauta*) the two dorsal arms are widely expanded, and secrete a delicate calcareous external shell, which is not connected by muscles with the body of the animal. The shell of the female Argonaut is one-chambered, spirally coiled and involute, its external border being keeled, and its surface tuberculated. The genus is represented in the Pliocene Tertiary by one or two species, and several living forms are known.

According to von Zittel, the genus *Acanthoteuthis* is founded upon the remains of an Octopod Cuttle-fish preserved in the fine-grained Lithographic Limestone (Jurassic) of Solenhofen, and showing the form of the body and the outline of the arms, the latter carrying each two rows of falciform horny hooks.

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